Electrophysiological Correlates of Performance Monitoring in Middle and Late Adolescence

by

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Abstract

The ability to monitor and evaluate the consequences of ongoing behaviors and coordinate behavioral adjustments seems to rely on networks including the anterior cingulate cortex (ACC) and phasic changes in dopamine activity. Activity (and presumably functional maturation) of the ACC may be indirectly measured using the error-related negativity (ERN), an event-related potential (ERP) component that is hypothesized to reflect activity of the automatic response monitoring system. To date, no studies have examined the measurement reliability of the ERN as a trait-like measure of response monitoring, its development in mid- and late- adolescence as well as its relation to risk-taking and empathic ability, two traits linked to dopaminergic and ACC activity. Utilizing a large sample of 15- and 18-year-old males, the present study examined the test-retest reliability of the ERN, age-related changes in the ERN and other components of the ERP associated with error monitoring (the Pe and CRN), and the relations of the error-related ERP components to personality traits of risk propensity and empathy. Results indicated good test-retest reliability of the ERN providing important validation of the ERN as a stable and possibly trait-like electrophysiological correlate of performance monitoring. Of the three components, only the ERN was of greater amplitude for the older adolescents suggesting that its ACC network is functionally late to mature, due to either structural or neurochemical changes with age. Finally, the ERN was smaller for those with high risk propensity and low empathy, while other components associated with error monitoring were not, which suggests that poor ACC function may be associated with the desire to engage in risky behaviors and the ERN may be influenced by the extent of individuals' concern with the outcome of events.

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General introduction

The brain implements a variety of cognitive processes, which need to function together efficiently. One such cognitive process is to monitor and evaluate the consequences of ongoing behaviors and coordinate behavioral adjustments. The anterior cingulate cortex (ACC), a brain structure located on the medial surface of the frontal lobes, may be a critical neurobiological substrate of successful performance monitoring. The ACC has rich interconnections with cortical and subcortical brain areas, including association cortex (dorsolateral prefrontal, ventromedial prefrontal, orbitofrontal and parietal), motor systems, subcortical limbic regions and the basal ganglia. Recent animal anatomical and electrophysiological evidence suggests that the ACC is relatively late to mature, perhaps not reaching optimal levels of functioning until young adulthood. Several neuroimaging studies have noted that hyperactivity of this region may reflect excessive response monitoring and concern over the outcome of an event, whereas hypoactivity of the ACC may reflect apathy or a lack of concern. Accordingly, adaptive cognitive and social behaviors are dependent upon the maturation and/or function integrity of this region.

Electrophysiological studies have identified the error-related negativity (ERN) as a possible index of response monitoring. The ERN is a component of the event-related potential (ERP) recorded from the scalp that typically occurs after the commission of an error. As such, the ERN may reflect activity of an automatic response monitoring system as well as affective responses to errors (e.g., distress, apathy). The ERN may be mediated by dopamine, the primary neurotransmitter of the frontal cortex, and reflect a reinforcement learning signal (i.e., the negative consequences of making an error). Individuals with high risk propensities and those lacking empathy may show diminished responsiveness to threat and/or errors when unfavorable outcomes are encountered (i.e., they are unable to experience or appreciate the emotional significance of errors or other unfavorable outcomes), and may be less likely to learn from past negative experiences. This diminished responsiveness may contribute to, and or serve to maintain maladaptive behaviors, and this may be reflected in the amplitude of the ERN. Thus, the examination of the error monitoring (vis-à-vis the ERN) developmentally, as well as in relation to affective style, may have implications for understanding the contribution of reinforcement learning deficits to risky and otherwise delinquent and antisocial behavior in adolescents. Furthermore, this is a technology that may be useful in monitoring the effectiveness of behavioral and/or psychopharmacological intervention programs. However, if this is the direction in which the research is going, it is crucial to examine the reliability the ERN. Reproducibility is important for investigating the underlying mechanisms of response monitoring and to assess just *how* useful a biological marker the ERN can be.

This research is divided into four chapters which present separate electrophysiological studies. Each of the four studies is based on data obtained from an initial sample of forty 15-year-old and fifty 18-year-old males. However, the sample size for each study is slightly different due to outliers on one or more measure used at the time and differences in data processing requirements. Each chapter has an introduction, hypotheses, results and specific conclusions. The first chapter presents a study examining the stability of error-related ERPs as an indirect measure of ACC activity (and will present the general method). In the second chapter, age-related changes in error-related ERPs are investigated. The third and fourth chapters then examine the relation between error-related ERPs and risk-taking and empathic behaviors (respectively). Finally, a general discussion points to future directions. Note the footnotes are presented together following the references.

Chapter I: Test-retest reliability of error-related ERPs in adolescents

The functional significance of the error-related negativity (ERN) still remains unclear, but researchers speculate that the ERN may reflect activity of an automatic response monitoring system and a trait-like measure of this system. However, no studies to date have examined the measurement reliability of error-related ERPs. The purpose of the present study was to examine the test-retest reliability of the ERN and the error-positivity (Pe) during a simple and more difficult speeded response task on two separate occasions. Thirty-one 15-year-old males completed identical flanker and go/no-go tasks on two occasions separated by 3 to 6 weeks. Participants showed similar arousal levels and response rates from time 1 to time 2. Results also indicated good test-retest reliability of the ERN and Pe. The ERN was most reliable when using a residualized ERN amplitude measure as opposed to a peak-to-peak or base-to-peak measure. The present study provides important validation of the ERN (and Pe) as a stable and possibly trait-like electrophysiological correlate of performance monitoring.

Introduction

The anterior cingulate cortex (ACC) appears to be activated in connection to the detection and appraisal of errors (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Devinsky, Morrell, & Vogt, 1995; Vogt, 1993). This response monitoring elicits a characteristic event-related potential (ERP) component, namely the error-related negativity (ERN; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). The ERN appears as a negative deflection in the response-locked ERP waveform peaking approximately 50-100 ms following errors. The ERN has a fronto-central scalp distribution and fMRI and source localization studies suggest the ERN may be generated by the caudal ACC (Carter et al., 1998; Dehaene, Posner, & Tucker, 1994; Falkenstein, Hoorman, Hohnsbein, & Blanke 1991; Van Veen & Carter, 2002).

The ERN has been widely used as an index of (1) automatic, general response monitoring vis-à-vis comparing behaviors against intended goals (Bernstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991; Falkenstein, et al., 2000); (2) conflict monitoring (Botvinick, Cohen, & Carter, 2004; Carter et al., 1998); and (3) state- and trait-like affective responses to errors (e.g., Hajcak, Moser, Yeung, & Simons, 2005; Hajcak & Simons, 2002; Luu, Collins, & Tucker, 2000; Pailing & Segalowitz, 2004a), with these processes being mutually compatible in most paradigms used to elicit ERNs. These cumulative findings suggest that the ERN should be stable across time. For example, if the ERN reflects automatic response and/or conflict detection, one would expect some trait-regularity in this process and the biological system subserving it. Additionally, longitudinal studies have demonstrated that most traits accounting for emotional, interpersonal, attitudinal, and motivational style (which influence the ERN), change little in absolute level and individual differences are strongly preserved over long periods of time (see for example, McCrae & Costa, 1984).

Because the direction of research in this field includes factors related to individual differences, we need to examine the reliability the ERN. Reproducibility is important for investigating the underlying mechanisms of response monitoring and to assess just how useful a biological marker the ERN can be. Some researchers suggest the ERN may reflect functional integrity and processing efficiency of the ACC across child development (e.g., Hogan, Vargha-Khadem, Kirkham, Baldeweg, 2005; Santesso, Segalowitz, & Schmidt, in press) as well as dopaminergic innervation of the prefrontal cortex (Holroyd & Coles, 2002; Segalowitz, Davies, & Gavin, 2004). Other researchers have used repeated-measure designs to examine biological factors, such as sleepiness, on response monitoring without first directly examining the stability of the ERN (e.g., Murphy, Richard, Masaki and Segalowitz, 2006; Scheffers, Humphrey, Stanny, Kramer, & Coles, 1999). To date, there appear to be no studies examining the test re-test reliability of the ERN and other components in the error-related ERP. The goal of the present study was to examine test-retest reliability of error-related ERP components on two separate occasions in a sample of adolescent males.

Less well studied is the error positivity (Pe), which is a late positive component peaking 200-500 ms after an error response. The Pe is maximal at a more posterior scalp location and may be generated by the sources in rostral ACC as well as in parietal regions (Kaiser, Barker, Haenschel, Baldeweg, & Gruzelier, 1997; Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002). The reliability of this component is also of interest as the Pe may reflect conscious evaluation of an error (Falkenstein et al., 1991, 2000; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000) and seems to be functionally distinct from the ERN (e.g., Bartholow et al., 2005; Murphy et al., 2006; Vidal et al., 2000).

A variety of factors may cause within-subject variability in ERP components. In a series of studies Polich demonstrated that the P300 is sensitive to a variety of biological and environmental factors, such as circadian rhythm, time of year, menstrual cycle, sleep deprivation, and common drugs (see Polich & Kok, 1995). Using repeated measures, this research has been extended to the ERN. For example, Murphy and his colleagues (2006) examined the effect of moderate sleep deprivation (i.e., after 22 hours of wakefulness) on error processing. The participants performed a standard visual flanker task on two occasions: before and after sleep deprivation. The authors reported similarity in the ERN across the two levels of alertness. However, there was a reduction in post-error evaluation as indexed by reduced Pe amplitude and a reduction in post-error slowing. The authors concluded that sleepiness might have reduced the motivation to adapt behavior even when errors were detected. Although this study was designed to examine the effects of sleepiness on error monitoring, it provided crude evidence for the stability of the ERN (but not the Pe) despite fatigue.

The present study examined the reliability of the ERN and Pe from one testing session to the next using both Pearson (*r*) and intraclass (*r'*) correlations. As noted by Segalowitz and Barnes (1993), Pearson *r* is appropriate when examining the linear relationship between two patterns of numbers as representing the stability of the ordering among subjects. The Pearson coefficient is adequate for examining the reliability between two scores with equal means and variations (and, in this case, it will equal the intraclass correlation). Intraclass *r'* is appropriate when examining psychometric stability - the consistency/homogeneity or agreement of the values obtained from one time to the next (Shrout & Fliess, 1979). If subjects' scores change by the same amount, it will not affect the Pearon correlation but will affect the intraclass correlation. Since subtle alterations in testing and the participant's state may affect the amplitude of the ERP components, we sought to minimize differences between sessions. We limited the study to males, tested participants at approximately the same time of day and season of year, and examined differences in baseline salivary cortisol levels as an index of central arousal (see Chapotot, Buguet, Gronfier, & Brandenberger, 2001). We hypothesized that the ERN would show good test-retest reliability and, precluding any differences in arousal state and/or recognition of errors from one testing session to another, the Pe would also be reliable.

Method

Participants

Data from 27 adolescent males were available for analysis at 2 time points. Participants were recruited from the community and tested as part of a larger study at Brock University (St. Catharines, Ontario). All participants were 15 years of age (M = 15.1, SD = .15) at the first study session and retested between 3 to 6 weeks later. Participants were Caucasian and the majority of the participants were right-handed. Each participant received $10 per hour for his participation.

Electrophysiological tasks

Flanker task. Participants completed a visual flanker task that consisted of a five-letter array of which the central letter was the target. Participants pressed a numerical keypad with the index finger of the left or right hand, corresponding to the target letters H or S (Eriksen & Eriksen, 1974). The target letter was flanked on each side by either congruent (SSSSS or HHHHH) or incongruent (HHSHH, SSHSS) letters. Congruent trials are typically associated with fewer errors and faster response times than incongruent trials (Eriksen & Eriksen, 1974). There were 80 congruent array trials and 160 incongruent array trials (for a total of 480 trials). Each array remained on the screen for 189 ms with an inter-stimulus interval (ISI) of 1243 ms.

Stimuli were randomized across trials and a rest break was given after every 160 trials. The same random ordering of stimuli was used for each participant. Stimuli were presented using E-Prime (Psychological Software Tools, Pittsburgh, PA).

Go/no-go task. Participants completed a visual go/no-go task similar to that used by Garavan, Ross, and Stein (1999) and Lewis, Lamm, Segalowitz, Stieben and Zelazo (2006). Two letters (e.g., x and y) were presented serially in an alternating pattern and participants were required to make a button press to each letter. Responses were to be withheld to the lure stimuli: a lure occurred when the alternation was interrupted (e.g., the fifth stimulus in the train x-y-x-y-y-x-y). Each stimulus remained on the screen for 97 ms with an initial inter-stimulus interval (ISI) of 1000 ms. The task was designed such that, after 2 consecutive no-go errors, the ISI increased by 107 ms, and after 2 consecutive correct responses, the ISI decreased by 53 ms. Participants completed three blocks of trials: the first block comprised the letters x and y, the second block u and d, the third block o and p. Lures were distributed unpredictably throughout the stimulus stream. The first and third blocks were each composed of 200 stimuli of which 66 were no-go lures while the second block was composed of 150 stimuli including 40 lures (totalling 550 trials, 172 lures). A rest break was given after each block of trials. Before this task, participants were allowed to complete a practice session of 30 trials using all three sets of letters and a total of 7 no-go lures. The same ordering of stimuli was used for each participant and presented using E-Prime (Psychological Software Tools, Pittsburgh, PA).

Electrophysiological recording and data reduction

EEG was recorded continuously using a 128-channel Electrical Geodesics system (EGI Inc, Eugene, OR) at 500 Hz with 0.1-100 Hz analog filtering referenced to the vertex (channel 129). Impedance of all channels was kept below 50 kΩ. Data were segmented and re-referenced off-line to linked-mastoids. EEG epochs were extracted beginning 600 ms before and ending 800 ms after each response for the midline sites Fz, FCz, Cz, Pz (channels 11, 6, 129, 62, respectively). Each trial was visually inspected for movement artifact and eye-movement artifacts were corrected by regression analysis.[1] The amplitude of the ERP was derived from each individual's average waveform (consisting of ten or more error trials) after smoothing with a nonphase-shifting single pass 17-point moving average (34 ms, approximately 3 db down at 15 Hz). A computer-assisted hand scoring peak-analysis program (Segalowitz, 1999) was used to quantify peak amplitude and latency of averaged ERP waveforms.

A pre-response baseline between -600 to -400 ms was used as this normally captured a pre-stimulus activation period as well as the previous trial's return to baseline. The P3 was measured as the most positive peak before the onset of the ERN on error trials. (This is not intended to be a measure of the P300 which is normally scored time-locked to the stimulus, whereas these ERP are time-locked to the response. Nevertheless, the positivity does reflect the same positivity as the classic P300 although it is usually somewhat attenuated because of the response-locking. For convenience, we will refer to it as the P3). The ERN was measured as the most negative peak in the time window of 20-150 ms after an incorrect key press. The peak-to-peak ERN was computed as the amplitude of the most positive peak before the onset of the ERN (i.e., the P3) minus the most negative peak (i.e., the ERN) in the time window of 20-150 ms after an incorrect key press. A measure similar to the peak-to-peak ERN, but with different statistical properties, is the residualized ERN which was calculated using regression to partial out the variability due to the P3 from the amplitude of the ERN. The Pe was measured as the second positive peak in the time window of 200-500 ms after an incorrect key press, i.e., we used the late Pe to avoid scoring the rebound after the ERN (Van Veen & Carter, 2002). Only data from incongruent error trials are presented here since participants did not commit enough errors on congruent trials to form ERP averages.

Salivary Cortisol Collection and Enzyme-Linked Immunoassay (EIA)

Upon arrival to the laboratory at each testing session, a baseline saliva sample was collected. Salivary cortisol was used because it is non-invasive and highly correlated with serum cortisol (Vining, McGinley, Maksvytis, & Ho, 1983). Each participant was given a bottle of water and asked to rinse his mouth thoroughly for 1 minute. The participant was then asked to wait 2-5 minutes before expectorating at least 1.0 ml of saliva into a sterile 1.5 ml Nalgene cryotube. The saliva samples were stored at -80° C until assayed.

All enzyme immunoassays were carried out on NUNC Maxisorb plates. Cortisol antibodies (R4866) and corresponding horseradish peroxidase conjugate were obtained from C. Munro of the Clinical Endocrinology Laboratory, University of California, Davis. Steroid standards were obtained from Steraloids, Inc. (Newport, Rhode Island). Plates were first coated with 50 μl of antibody stock diluted at 1:8500 in a coating buffer (50 mmol/l bicarbonate buffer pH 9.6). Plates were sealed and stored for 12–14 h at 4 °C. 50 μl wash solution (0.15 mol/l NaCl solution containing 0.5 ml of Tween 20/l) was added to each well to rinse away any unbound antibody, then 50 μl phosphate buffer per well was added. The plates were incubated at room temperature for 2 hours before adding standards, samples, or controls. For each hormone, two quality control salivary samples at 30% and 70% binding (the low and high ends of the sensitive range of the standard curve) were prepared. Next, 50 μl cortisol horseradish peroxidase conjugate were added to each well, with 50 μl of standard, sample, or control. After plate loading, plates remained incubated for 1 h. The plates were then washed with 50μl wash solution and 100μl of a substrate solution of citrate buffer, H_2O_2 and 2,2′-azino-bis [3-ethylbenzthiazoline-6-sulfonic acid) was added to each well and the plates were covered and incubated while shaking at room temperature for 30–60 min. The plates were then read with a single filter at 405nm on the microplate reader (Titertek multiskan MCC/340). Blank absorbances were obtained, standard curves generated, a regression line was fit to the sensitive range of the standard curve (typically 40 – 60 % binding) and samples were interpolated into the equation to get a value in pg per well. Each sample was assayed in duplicate and averages were used. Interplate variation (CV) was 6.45% while intraplate variation was 6.51%.

Behavioral Measurements

Response time was calculated from stimulus onset to button press, with averages based on responses greater than 100 ms and less than 1000 ms. Post-error slowing was used an index of error recognition and response adjustment and was calculated as the average response time for correct trials following error trials minus the average response time for correct trials following other correct trials.

Probability values for all analyses with repeated measures utilized the Greenhouse-Geisser correction, with original degrees of freedom reported. All procedures conformed to the ethical principles of the Canadian Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans and were approved by the Research Ethics Board of Brock University.

Results

Salivary Cortisol

In order to determine whether the arousal level of the participants differed significantly from one testing session to the next, we analyzed baseline levels of salivary cortisol. First, we wanted to make sure that salivary cortisol was a reliable measure over time. We ran a Pearson correlation and found that baseline salivary cortisol was significantly related at time 1 and 2, r

= .40, p = .04. Reliability was also confirmed by an intraclass correlation analysis, $r' = .39$, p = .02. Second, a paired t-test confirmed there were no significant differences in participants' mean salivary cortisol levels from time 1 to 2, $t(25) = 1.12$, $p > .20$.

Behavioral data

The means and standard deviations for response time (RT), standard deviation of RT, accuracy and post-error slowing for the flanker task are presented in Table 1.1 and for the go/no-go task in Table 1.2.

Flanker task. In order to examine accuracy across time, we performed an ANOVA with Category (congruent, incongruent) and Time (time 1, time 2) as within-subjects factors. The ANOVA revealed a significant main effect for Category [$F(1, 25) = 22.87$, $p < .001$] such that participants made more incongruent than congruent errors at each time. The participants' error rate decreased from time 1 to time 2 but this failed to reach significance ($p = .17$). A similar ANOVA was performed to examine response times with Category (congruent, incongruent) Response (correct, error) and Time (time 1, time 2) as the within-subjects factors. We found a significant main effect for Category [$F(1, 25) = 12.30$, $p = .002$] such that RTs were faster for congruent compared with incongruent trials. A significant main effect for Response [$F(1, 25) = 56.72$, $p < .001$] indicated that RTs were faster for error than correct trials. Finally, there was a significant main effect for Time [$F(1, 25) = 4.40$, $p = .05$] indicating that RTs during the task were slower at time 2 than at time 1. A similar ANOVA was performed to examine the variability in response times (i.e., standard deviation of RT). There was a significant main effect for Category [$F(1, 25) = 12.30$, $p = .002$] and Response [$F(1, 25) = 23.95$, $p < .001$] indicating that response times were more variable for incongruent trials and error trials. There was also a significant Category by Response interaction [$F(1, 25) = 4.47$, $p = .04$] indicating that congruent error trials were less variable than congruent correct trials compared with incongruent error and correct trials. No other main effects or interactions were found which supports that participants used a steady response style across time.

An ANOVA with Category and Time was also performed to examine post-error slowing. As can be seen in Table 1.1, participants showed post-error slowing at time 1 but not at time 2. We found a significant main effect for Time [$F(1, 25) = 9.84$, $p = .004$] indicating that post-error slowing occurred for both incongruent and congruent categories at time 1 but not at time 2.

We also performed a series of Pearson correlations to examine the relations between accuracy and RTs at time 1 and time 2 for the flanker (and go/no-go task; see Table 1.3). There was no relation between the percentage of congruent and incongruent errors committed across sessions. However, RTs for congruent ($r = .49$, $p = .01$) and incongruent ($r = .48$, $p = .01$) correct trials were significantly related across sessions, while incongruent errors were marginally related ($r = .36$, $p = .07$).

Go/no-go task. An ANOVA with Response and Time as within-subjects factors revealed no significant relations. As can be seen in Table 1.3, individual differences in accuracy and RTs for correct and error responses were maintained significantly across sessions. This could be important because the ERPs are time-locked to the responses. We also examined standard deviation of RT using a similar ANOVA but there were no significant main effects nor was there an interaction, indicating participants' response time did not vary across time.

Finally, a paired *t*-test indicated that participants made significantly more errors (percentage of errors) on the go/no-go task compared with the flanker task at time 1, $t(18) = 2.2$, $p = .04$, and at time 2, $t(17) = 4.9$, $p < .01$, suggesting that the go/no-go task was more difficult to perform.

Test-retest reliability of error-related ERPs

We calculated Pearson r and the intraclass correlation (r') to examine similarity between each participant's ERPs at time 1 and time 2. The r' (single measures) was obtained using SPSS reliability analysis and specifying a one-way random model. r's were computed separately for the ERP averages at each site. While tasks designed for clinical assessments require values of at least .9 for individual reliability, experimental research based on groups can be adequate with correlations of only at least .50 (Helmstadter, 1964).

The means (SD) for the P3, ERN and Pe for the flanker and go/no-go task at time1 and time 2 are presented in Table 1.4 and 1.5, respectively. Tables 1.6 and 1.7 display the Pearson (r) and intraclass (r') correlations for the flanker task and go/no-go task, respectively. In order to ensure that the reliability of the ERN was not affected by variance in the P3 over testing sessions, we calculated the correlations using three different scoring methods for the ERN: base-to-peak, peak-to-peak, and the residualized ERN (see Method section for details).

Flanker task. We performed an ANOVA with Site (Fz, FCz, Cz, Pz) and Time (time 1, time 2) as within-subjects factors for the P3, ERN and Pe. For the P3, there was a significant main effect for Site [$F(3, 78) = 12.4, p < .01$]. As seen in Table 1.4, the P3 was maximal at Pz. No other significant results were found. For the base-to-peak ERN, there was a significant main effect for Site [$F(3, 72) = 29.14, p < .01$] with the ERN maximal at FCz. There was also a significant Site by Time interaction [$F(3, 72) = 3.97, p = .04$] indicating greater reduction in the ERN amplitude at FCz and Cz (reaching marginal significance, p=.07), compared with Fz and Pz ($p > .20$). We noted a significant positive correlation between the P3 and ERN at each site (r-values ranged from .77 to .44 with p-values ranging from < .001 to .02). Since the correlations between the P3 and ERN were not perfect and the P3 itself was not highly reliable changes in the ERN across time *could* be influenced by variation in the P3. To account for this potential problem, we analyzed the residualized ERN, which partials out the amplitude of the P3 from the amplitude of the ERN. An analysis with the residualized ERN yielded no significant main effects or interaction, and it appeared that the ERN was maximal at FCz. Using the peak-to-peak method, an ANOVA revealed a significant main effect for time [$F(1, 24) = 5.92, p = .02$] such that across all sites, there was a reduction in ERN amplitude from time 1 to time 2. There was also a significant main effect for Site [$F(3, 72) = 27.22, p < .01$] with the ERN maximal at Cz. A significant Site by Time interaction [$F(3,72) = 3.93, p = .01$] indicated that the ERN decreased at Fz, FCz, and Cz from time 1 to time 2, but not at Pz. Using this method of scoring, however, it is impossible to tell whether variability in the P3 was contributing to these effects. Finally, for the Pe, there was a significant main effect for Site [$F(3, 72) = 32.14, p < .01$], with the Pe maximal at Pz. No other significant results were found.

The intraclass correlations for the ERN using the residualized and peak-to-peak ERN were highest at FCz then Cz, with the residualized ERN at FCz yielding the highest intraclass correlation (see Table 1.6). Both the Pearson and intraclass correlation coefficients at FCz, were greater than .50 indicating a large effect size (Cohen, 1977). The ERN measured by the base-to-peak method performed poorly. For the Pe, the intraclass correlations were significant at Pz and Cz, with the values at Cz appearing more reliable. Figure 1.1 displays the averaged response-locked ERP waveforms at time 1 and time 2 for the flanker task. As can be seen, there is considerable overlap in the averaged ERP waveforms.

Finally, a series of Pearson correlations revealed that there was no relation between ERN amplitude, response time or accuracy.

Go/no-go task. We performed an ANOVA with Site and Time as within-subjects factors for the P3, ERN and Pe. For the P3, there was a significant main effect for Site [$F(3, 57) = 4.18, p = .03$]. As seen in Table 1.5, the P3 was maximal at Pz. There was also a significant Site by Time interaction [$F(3, 57) = 5.01, p = .01$], indicating that the amplitude of the P3 decreased at Pz only whereas there were increases in the P3 at all other sites from time 1 to time 2. For the base-to-peak ERN an ANOVA revealed a significant main effect for Site [$F(3, 60) = 20.39, p < .01$] with the ERN maximal at FCz. Again, we found significant positive correlations between the P3 and ERN at each site (r-values ranged from .87 to .68 with p-values < .001). The residualized ERN yielded a marginally significant main effect for Time [$F(1, 18) = 3.81, p = .07$], with larger values at time 1. An ANOVA with the peak-to-peak ERN yielded a significant main effect for Time [$F(1, 18) = 6.50, p = .02$] indicating that across all sites there was an increase in the ERN amplitude from time 1 to time 2, which is probably due to the changes in the P3. Paired t-tests revealed that the increase in the ERN was only significant at Fz and Cz (p= .01 and $p = .03$, respectively). There was also a significant main effect for Site [$F(3, 54) = 21.03, p < .01$] with the ERN maximal at FCz. For the Pe, there was a significant main effect for Time [$F(1, 24) = 6.67, p = .02$] such that across all sites the Pe decreased in amplitude from time 1 to time 2. There was also a significant main effect for Site [$F(3, 72) = 41.97, p < .01$] indicating the Pe was maximal at Pz. There was no significant interaction between Time and Site indicating that at the posterior sites (where the Pe is usually scored), there was no significant reduction in the Pe.

As can be seen in Table 1.7, the intraclass correlations for the ERN using the residualized and peak-to-peak ERN were significant at FCz and Cz. The base-to-peak and residualized ERN appeared to yield the highest reliabilities. The intraclass correlations for the Pe were significant and highest at Cz then Pz. A large effect size for the Pearson and intraclass correlations were found at Cz and Pz. Figure 1.2 again displays considerable overlap in the averaged response-locked ERP waveforms at time 1 and time 2 for the go/no-go task.

In order to ensure that differences in performance from time 1 to 2 were not contributing to the results, we performed a series of Pearson correlations between the behavioral measures and the ERN. Results revealed no significant relations between ERN amplitude, response time and accuracy.

Discussion

The purpose of the present study was to provide the first demonstration of the reliability of error-related ERPs (ERN and Pe) during a simple and more difficult speeded response task on two separate occasions in a large sample of healthy adolescent males. As noted by Segalowtiz and Barnes (1993), variance in ERP components can arise from variables neither manipulated nor measured by the experimenter (e.g., arousal) and from inherent unreliability of the measure, such as identification of and measurement of the ERP component peaks or instability in its generation. We attempted to minimize this variance by limiting the study to males (i.e., due to possible hormonal variation effects on ERPs during menstrual cycles) of the same age and test each participant at approximately the same time of day and season of the year. Baseline salivary cortisol levels also suggested that participants' central arousal level was comparable before ERP testing on the first and second occasions.

Participants found the go/no-go task to be more challenging than the flanker task as reflected by higher error rates for this task during each session. Individual differences in response times were significantly correlated between time 1 to time 2, and responses times slowed in the flanker task during the second testing session. Participants' performance also slightly improved on each task during the second session. This suggests that participants made a speed-accuracy trade-off and responded more cautiously at time 2, despite instructions emphasizing both. However, there were no changes in the variability of response times across sessions indicating that participants maintained a similar response style, and decreases in the ERN could not be due to variability in response times (i.e., latency jitter). There was no post-error slowing for the flanker task at time 2, but this may be due to overall slowing. Although previous research has shown that task difficulty does not affect the amplitude of the ERN (e.g., Pailing and Segalowitz 2004b), response control might. We reported that individuals who made more impulsive errors displayed smaller ERN amplitudes compared with those who used a more cautious strategy during the task and avoided making impulsive errors (Pailing, Segalowitz, Dywan, & Davies, 2002). In the present study, the ERN was not related to response time, response time variability or accuracy suggesting the reduction in the ERN amplitude from time 1 to time 2 might have been due to habituation, boredom or other changes across time.

We also report for the first time that the ERN and Pe show good test-retest reliability during a simple and more difficult visual speeded response task. For each task, the ERN was maximal at the fronto-central sites whereas the Pe was maximal at centro-parietal sites. Large effect sizes at these sites were found for the Pearson and intraclass correlation for the ERN and Pe (Cohen, 1977). These relations were preserved despite what appeared to be a slight attenuation in the ERN amplitude during the flanker task (but not the go/no-go task) from time 1 to time 2. This attenuation may have been due to habituation to the relatively simple task and/or participant boredom. These ERP findings suggest that the ERN and Pe may reflect trait-like measures of performance monitoring. The Pe, however, may be less stable depending on participants' arousal state (Murphy et al., 2006) but more studies are needed to examine the effects of various biological and environmental factors on this component.

It is interesting to note the relations between error rate and ERN amplitude in our data. There is some concern amongst researchers that an increase in error rate may make the experience less salient and therefore reduce the amplitude of the ERN component that arises from it. We generally find that the number of errors a person makes does not correlate with the amplitude of their ERN (Pailing & Segalowitz, 2004a,b; Santesso, Segalowitz & Schmidt, in press), and we have shown that manipulating the error rate within subject by increasing the number of choices on a flanker task does not alter the ERN amplitude (Pailing & Segalowitz, 2004b). In the current data set, we also find that the number of errors within session and task does not correlate with the ERN amplitude. Even more interesting, we found despite making fewer errors during the second session than the first on the flanker task, the ERN amplitude diminished. This reinforces the disconnection between number of errors and ERN amplitude.

Scoring methods

Debate remains in the field regarding which scoring method (e.g., base-to-peak, peak-to-peak) provides the best measure of the ERN (i.e., uncontaminated by variability in stimulus evaluation indexed by the P3). Here, we examined three different scoring methods in order to determine which method was the most reliable, and possibly provide insight into which method should be used. For the sites of interest, we found that, for the most part, the intraclass correlation was higher when using a residualized ERN (i.e., the amplitude of the ERN with the variance due to the P3 preceding it partialled). The peak-to-peak method did, however, demonstrate adequate reliability whereas the base-to-peak method performed poorly. Future studies may wish to include the residualized ERN in addition to more traditional methods like the peak-to-peak. The superior reliability for peak-to-peak measurements over baseline-to-peak scores does not guaranty greater validity since the increased reliability may be due to variance in the P3. Indeed, the P3 was reliable for the flanker task (but not the go/no-go task). These values were lower compared with the reliability of auditory P3s reported by Segalowitz and Barnes (1993), but these authors used stimulus-locked ERPs. The use of response-locked ERPs in the present study, and consequential response jitter, may have contributed to lower reliability scores.

The present study is not without limitations. First, in order to control for possible hormonal variation between participants and across testing sessions, we limited our studies to males. However, the effects of hormones over the course of the female menstrual cycle are not limited to sexually relevant stimuli, but may influence early and late ERP components (such as the P3) to emotional and neutral stimuli (e.g., Krug, Plihal, Fehm, & Born, 2000; Walpurger, Pietrowsky, Kirschbaum, & Wolf, 2004). For example, in a recent study, O'Reilly and colleagues examined the P3 in response to visually presented words during the menses (when estrogen and progesterone are low) and ovulatory phase (when estrogen and progesterone are high) of the menstrual cycle (O'Reilly, Cunningham, Lawlor, Walsh, & Rowan, 2004). The authors reported that the amplitude of the P3 was higher at menses compared to the ovulatory phase and there were no differences in accuracy and response time. The authors suggested that progesterone might attenuate the P3 as progesterone has been found to decrease brain excitability (Holzbauer, 1976) and have an inhibitory effect on cognition (e.g., Sherwin, 1988). Considering mood may be influenced throughout the menstrual cycle (e.g.,Collins, Eneroth, & Landgren, 1985) future studies should examine how hormonal variation affects the ERN. Segalowitz, Davies and Gavin (2004) also suggested that gender differences in the ERN throughout late childhood and adolescent might be due to the development of the dopamine and reproductive system (or an interaction of the two). The effect of hormonal variation on the ERN and the P3 (especially since this component is often used in scoring the ERN) in males and females across development needs further examination. Second, participants were 15 years of age. Adolescence is a transformational period of development during which complex interactions occur among human systems at multiple levels, including personality. McCrea and

Costa (1984) note that affective style becomes more stable after 18 years of age. Continued affective and hormonal development may interact and affect optimal development of and functional integrity of the response monitoring system. Although this suggests that the ERN may become *more* stable in young adulthood, future studies may wish to examine the reliability of error-related ERPs in an adult population with both male and female participants. It may also be the case that 15 year olds may present a sample with greater variability across individuals than would be present amongst an adult sample, because of variation in the stage of growth at the time of testing. This increased cross-subject variation, assuming no increased within-subject variation, would strengthen the retest reliability. In either case, the current values should not be fully generalized to adults without further testing.

In summary, the present study provides much needed evidence for the reliability of error-related ERPs. Reproducibility of the ERN suggests it may reflect a trait-like measure and therefore be a useful tool for investigating the response monitoring system (and ACC). Furthermore, results from the present study provide some assurance regarding the stability of the ERN for its use in longitudinal and repeated-measures designs.

Chapter II: Developmental differences in error-related ERPs in middle and late adolescent males

Although there are some animal studies documenting structural brain changes during late adolescence, there are few showing functional brain changes over this period in humans. Of special interest would be functional changes of the medial frontal cortex reflective of response monitoring. In order to examine such age-related differences, we analyzed event-related potentials to errors in a visual flanker task and a go/no-go task in adolescent males, 15 and 18-19 years old. Response times and accuracy were comparable between groups on each task but the younger group made more go/no-go errors, suggesting this task was more difficult. The error-related negativity, thought to be generated in the anterior cingulate cortex (ACC), had greater amplitude for the older adolescents on both tasks, and thus the difference is not due to performance levels. Results from this study suggest that the ACC, which supports response monitoring, is late to mature due to either structural or neurochemical changes with age.

Introduction

Dopamine is critical for complex cognitive functions such as emotional regulation, judgment and inhibitory control, many of which are associated with the prefrontal cortex (PFC). It is also associated with activity of the anterior cingulate cortex (ACC), which plays an important role in processing signals reflecting self-monitoring of one's own performance (Ridderinkhof, van den Wildenberg, Segalowitz & Carter, 2004). Of special interest is the notion that the reward circuitry of the brain (including prefrontal and limbic regions as well as the ACC) may differ between adolescents and adults and there may be a greater degree of over- production and elimination of dopamine receptors in males compared with females (Andersen, Thompson, Krenzel, & Teicher, 2002; Andersen, Rutstein, Benzo, Hostetter, & Teicher, 1997). These dopaminergic changes may have profound effects on adolescent behavior (especially in males) such as the increased need to seek out novel, risky activities and make decisions on the basis of immediate reward (see Spear, 2000, for review). Fortunately, we have a non-invasive reflection of the dopamine activity in the ACC in the context of performance self-monitoring in the event-related potential (ERP), known as the error-related negativity (ERN). Other components of performance monitoring ERPs are also available but may not have the same developmental trajectory. The purpose of the present study was to see whether there are developmental changes during late adolescence in the ERP specific to performance monitoring associated with ACC functioning.

Electrocortical and neural correlates of performance monitoring. The ability to detect and react to errors and adjust performance appears to involve the ACC (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Devinsky, Morrell, & Vogt, 1995; Vogt, 1993). This response monitoring elicits the ERN (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000), a negative deflection in the response-locked ERP waveform peaking approximately 50-100 ms following inappropriate responses (e.g., errors) and when the outcome of an event is worse than expected (Holroyd & Coles, 2002). The ERN has a fronto-central scalp distribution and source localization studies suggest the ERN is generated by the caudal ACC (Dehaene, Posner, & Tucker, 1994; Falkenstein, Hoorman, Hohnsbein, & Blanke 1991; Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002).

The functional significance of the ERN remains unclear. One hypothesis is that the ERN reflects the activity of a generic response monitoring system that detects errors by signalling a mismatch occurring between the intended and the observed response (Bernstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991). A second hypothesis is that the ERN reflects conflict arising from coactivation of both correct and error response channels on error trials (Carter et al., 1998), although conflict might constitute one part of the more generic monitoring system (Botvinick, Cohen, & Carter, 2004). Finally, the ERN may reflect affective responses to errors as the ERN is influenced by affective and motivational influences (e.g., Hajcak, McDonald, & Simons, 2003; Luu, Collins, & Tucker, 2000; Pailing & Segalowitz, 2004a).

Holroyd and Coles (2002) proposed a biochemical model of the error processing system implicating the mesencephalic dopamine system in the production of the ERN. Upon error commission (or errors in the prediction of a future salient event), the mesencephalic dopamine system conveys a negative reinforcement learning signal (i.e., absence of positive feedback/reinforcer) to the frontal cortex where it generates the ERN by "disinhibiting the apical dendrites of motor neurons in the ACC. The error signals are used to train the ACC, ensuring that control over the motor system will be released to a motor controller that is best suited for the task at hand" (p. 679). Accordingly, the model proposes that the size of the ERN is a function of the size of the dopaminergic error signal – the larger the ERN, the larger the signal.

Two recent drug trial studies have provided support for this biochemical model of the ERN. First, Zirnheld and colleagues examined the effects of haloperidol, a dopamine antagonist, on ERN amplitude (Zirnheld et al., 2004). The authors reported that the ERN was less pronounced at the central site in individuals administered haloperidol. Second, de Bruijn and colleagues reported an increase in ERN amplitude with administration of the stimulant amphetamine (de Bruijn, Hulstijn, Verkes, Ruigt, & Sabbe, 2004). Notably, the stimulating properties of amphetamine appeared limited to the error monitoring system, as information processing in general was not affected.

Changes in the dopamine system observed throughout development may have a robust influence on response monitoring (Lewis, 1997). Animal and human studies support anatomical and physiological maturation of the PFC and the ACC (Chugani, 1994; Cunningham, Bhattacharyya, & Benes, 2002; Huttenlocher, 1979), including increased dopaminergic innervation and metabolism, into early adulthood (Benes, Vincent, Molloy, & Khan, 1996; Kalsbeek, Voorn, Buijs, Pool, & Uylings, 1988; Lambe, Krimer, & Goldman-Rakic, 2000; Rosenberg & Lewis, 1995; Verney, Berger, Adrien, Vigny, & Gay, 1982). In the PFC, it has been reported that there is a large developmental increase in the dopaminergic innervation reaching its highest level during puberty (Lambe et al., 2000). As well, there are dramatic changes in dopamine receptor density during adolescence including marked overproduction and elimination of synapses and receptors during adolescence (Anderson, Classey, Conde, Lund, & Lewis, 1995; Lewis, 1997). This developmental pattern may also extend to the ACC.

Two other error-related ERP components have been less well studied compared with the ERN. First, the Pe is a late positive component peaking 200-500 ms after an error response. The Pe is maximal at a more posterior scalp location and may be generated by the rostral ACC as well as parietally (Kaiser, Barker, Haenschel, Baldeweg, & Gruzelier, 1997; Herrmann et al., 2004; Van Veen & Carter, 2002). The Pe may reflect conscious evaluation of an error (Falkenstein et al., 1991, 2000; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000) and seems to be functionally distinct from the ERN (e.g., Bartholow et al., 2005; Murphy, Richard, Masaki and Segalowitz, 2006; Vidal et al., 2000). Second, the correct-related negativity (CRN) is a negative deflection occurring on correct trials within the same time-window of the ERN and has similar morphological and topographical properties as the ERN (Vidal et al., 2000), although no source localization studies to date have confirmed that the ERN and CRN have similar generators. The CRN may reflect uncertainty about the correctness of a response (Scheffers and Coles, 2000) as the CRN and ERN become more similar to each other in magnitude when task difficulty and subjective ratings of uncertainty increase (Hogan, Vargha-Khadem, Kirkham, & Baldeweg, 2005; Pailing and Segalowitz, 2004b).

Developmental studies. In addition to the anatomical and physiological evidence for relatively late maturation of the PFC and the ACC, a few electrophysiological studies have examined developmental differences in response monitoring in childhood and adolescence. The first comprehensive study was conducted by Davies, Segalowitz and Gavin (2004) and examined error-related ERPs in individuals aged 7 to 25 years. These authors reported that on error trials, the ERN amplitude increased with age (and appeared to steadily increase in amplitude from about age 10 onward) while the Pe amplitude did not change with age. On correct trials, the CRN amplitude decreased during adolescence. Ladouceur, Dahl and Carter

(2004) examined the ERN and Pe in adolescents and found that the ERN was enhanced in older adolescents despite the small sample size, but there were no age differences in the Pe. Ladouceur and colleagues did not report CRN findings. Santesso, Segalowitz and Schmidt (in press) examined error-related ERPs in a larger sample of 10-year-old children and young adults (aged 18-30 years) using a similar flanker task. Consistent with Davies et al. (2004), 10-year-old children had smaller ERNs than adults, with no between-group differences on the Pe, and some ambiguity concerning the CRN (depending on the scoring method used). Children made more errors than adults but there were no group differences in post-error slowing. Taken together, these results provide electrophysiological support either for late maturation of the ACC or late involvement of the ACC in response monitoring. Davies et al. (2004) argued the absence of a strong ERN during childhood might be due to a slowly developing mesencephalic dopaminergic system and/or a structural immaturity of the ACC. Results also suggest there is some functional independence of response-monitoring ERP components. Whereas the ERN is immature in 10-year-old children, the Pe and CRN are fairly mature in children and adolescents.

In another developmental study, Hogan and colleagues (Hogan et al., 2005) examined the ERN and CRN in adolescents (aged 12-18 years) and adults (aged 18-22 years) using two tasks differing in complexity. The authors argued that changes in the ERN must be observed in the absence of performance differences between groups to support the notion that the neural generators of the ERN are immature. Otherwise, any group differences could be attributed to changes in task performance. The authors reported that the ERN was smaller for adolescents than for adults only for the complex task with no significant group differences in the Pe or CRN (although the CRN increased with task complexity). Additionally, the amount of post-error slowing increased with age but only for the complex task. Hogan and colleagues concluded that the absence of group differences in the ERN for the simple task did not support the hypothesis that this component is immature during adolescence. Alternatively, other frontal brain regions that exert influence over the ACC (particularly during increased task demands) may be immature. Again, this study was limited by a small sample size.

The purpose of the present study was to examine the ERN, Pe and CRN in a larger sample of healthy males in middle and late adolescence[2] using a visual flanker task and visual go/no-go task. Although both tasks require overriding prepotent responses, the flanker task elicits interference errors whereas the more difficult go/no-go task elicits errors of response inhibition. We were interested in whether the response monitoring system is similarly engaged for different types of errors and whether age-related changes are comparable for the two tasks. The younger group were 15 years of age, which corresponds to the median age of the adolescent groups examined by Ladouceur, Hogan and colleagues, while the older group were 18-19 years, the age at which we might expect maximum dopamine activity (Kalsbeek et al., 1988; Rosenberg & Lewis, 1995). Examination of error-related ERPs at these stages may provide important insights into (1) the role of the ACC in response monitoring during a period associated with continued development in the dopaminergic system and frontal lobe, and (2) the functional independence of error-related ERP components. We predicted that 15-year-olds would exhibit a significantly smaller ERN response compared with the 18-year-olds, while showing no difference in the Pe or CRN. We also predicted these results would be similar across tasks.

Method

Participants

Data from 39 older and 35 younger adolescent males were available for analysis. Older adolescents were recruited from Brock University (St. Catharines, Ontario) and ranged in age from 18 to 19 years (M = 18.54, SD = .71) while younger adolescents were recruited from the surrounding community and were 15 years of age (M = 15.03, SD = .17). Participants were Caucasian and the majority of the participants were right-handed (95%). Each participant received $10 per hour for his participation.

Electrophysiological tasks

Participants completed the flanker task and go/no-go task described in Chapter I, page 7.

Electrophysiological recording and data reduction

All recording and data reduction procedures were identical to those described in Chapter I, page 8. The CRN is a negative deflection occurring on correct trials within the same time-window of the ERN. The CRN was measured as the amplitude of the positivity preceding the CRN (i.e., the P3) minus the CRN on correct trials.

Behavioral Measurements

The behavioral measurements used for this study were identical to those described in Chapter I, page 11.

Results

Behavioral data

The means and standard deviations for response time (RT), RT variability and accuracy during the flanker task are presented in Table 2.1 and during the go/no-go task in Table 2.2.

Flanker task. To examine accuracy (percentage of errors) during the flanker task, an ANOVA was performed with Category (congruent, incongruent) as a within-subjects factor and Group (younger, older) as a between-subjects factor. Analyses revealed a significant main effect for Category [$F(1, 72) = 34.94, p < .001$], indicating that both groups made a greater percentage of errors on incongruent compared with congruent trials. No other significant results were found. In order to analyze age differences with regard to RT, we performed a Category by Response (correct, error) by Group ANOVA. We found significant main effects for Category [$F(1, 72) = 24.14, p < .001$] and Response [$F(1, 72) = 81.54, p < .001$], reflecting the fact that both groups of participants had faster RTs for the congruent compared with incongruent category and on error compared with correct trials. No other significant effects were found.

A similar ANOVA was performed for the standard deviation of response times (i.e., RT variability). We found a significant main effect for Category [$F(1, 68) = 4.75, p = .03$] and Response [$F(1, 68) = 39.61, p < .001$] indicating that RTs were more variable for incongruent (versus congruent) and error (versus correct) trials over all participants. There was also a significant Category by Group interaction [$F(1, 68) = 4.18, p < .05$] indicating that there was greater difference in variability between congruent and incongruent trials for 15-year-olds compared with 18-year-olds. No other significant effects were found. Importantly, independent samples t-tests revealed that RT variability did not differ between groups on incongruent error trials, something which could have contributed to attenuation of the waveform because they are time-locked to the response.

We also examined post-error slowing for the incongruent trials, which reflects recognition of the error and possibly an attempt to adjust response mode (Falkenstein et al., 2000). We performed an ANOVA with Response (correct following correct, correct following error) as the within-subjects factor and Group as a between-subjects factor. Both groups showed post-error slowing [$F(1, 72) = 8.83, p < .01$], with no difference between groups.

Go/no-go task. An independent samples t-test was performed to examine group differences in accuracy. We found that the younger adolescents made significantly more incorrect responses on no-go trials than the older ones, $t(71) = 2.31, p = .02$). A Response by Group ANOVA indicated that RTs were similar for incorrect no-go and correct go trials and there were no significant differences between groups for response time. A similar ANOVA examining RT variability revealed a significant main effect for Response [$F(1, 71) = 5.01, p = .03$], indicating that the RTs for correct go trials were more variable than the RTs for error trials. No group differences were found.

In a comparison of accuracy across tasks, a Task by Group ANOVA yielded a significant main effect for Task [$F(1, 59) = 21.91, p < .001$] indicating that participants committed more errors on the go/no-go task (32% error rate) compared with the flanker task (19% error rate).

Age-Related Differences in ERPs components

The means and standard deviations for the ERN, Pe and CRN amplitudes at each site for incongruent trials during the flanker task are presented in Table 2.3 and during the go/no-go task in Table 2.4.

The ERN: Flanker task. To examine age-related differences in the flanker task ERN, we performed a mixed ANOVA of Site (Fz, FCz, Cz, Pz) by Group. Analyses revealed a significant main effect for Site such that, for both groups, the ERN was maximal at FCz, followed by Cz, Fz, and Pz [$F(3, 204) = 54.1, p < .001$, see Figure 2.1]. There was also a significant main effect for Group [$F(1, 68) = 4.03, p = .05$], indicating that 18-year-olds had larger ERNs than 15-year-olds. Independent samples t-tests confirmed that adults had larger ERNs at FCz [$t(68) = 2.4, p = .02$] and Cz [$t(68) = 2.0, p = .04$].

We also examined the size of the ERN amplitude as a difference from the positivity preceding it (P3-to-ERN) given that variation in the positivity preceding the ERN (i.e., the P3 to the stimulus) may influence findings (see Pailing, Segalowitz, Dywan, & Davies, 2002; Santesso et al., in press). Again we found a significant main effect for Site [$F(3, 201) = 70.2, p < .001$] with the ERN maximal at Cz, followed by FCz, Fz and Pz. There was also a significant main effect for Group [$F(1, 67) = 4.1, p = .05$] as before, reaching marginal significance at Fz [$t(67) = 1.9, p = .06$], and significance at FCz [$t(67) = 2.0, p = .05$] and Pz [$t(67) = 2.2, p = .03$]. Similar results were found when we calculated a residual ERN amplitude using regression to partial out the variability due to the P3. Note that groups did not differ significantly in P3 amplitude at any site indicating the ERN difference between groups was due to its variability and not that of the stimulus evaluation indexed by the P3.

The ERN: Go/no-go task. Identical analyses to those described above were performed to examine age-related differences in the ERN during the go/no-go task (see Figure 2.2). There was a significant main effect for Site [$F(3, 216) = 53.4, p < .001$], indicating the ERN was maximal at FCz, followed by Cz, Fz and Pz. As can be seen in Figure 2.2, there was a significant main effect for Group [$F(1, 72) = 8.9, p = .004$] with 18-year-olds displaying larger ERNs than 15-year-olds, reaching significance at FCz [$t(72) = 2.6, p = .01$], Cz [$t(72) = 3.1, p < .01$] and Pz [$t(72) = 2.6, p = .01$].

Again, groups did not differ significantly in P3 amplitude at any site. Still, we examined age-related differences in the P3-to-ERN and residualized ERN amplitudes. For the P3-to-ERN, there was a significant main effect for Site [$F(3, 210) = 37.9,\ p < .001$] with the ERN maximal at FCz, and significant main effect for Group [$F(1, 70) = 10.4, p = .002$] with

18-year-olds displaying larger ERNs than a15-year-olds. Independent samples t-tests showed that this difference was significance at all sites ($p <= .01$). For the residualized ERN, there was a main effect for Group [$F(1, 70) = 12.45, p = .001$] such that 18-year-olds had larger ERNs than 15-year-olds at each site ($p <= .03$).

The Pe: Flanker task. A separate ANOVA was performed to investigate age-related differences in the Pe. Note that the total sample size was reduced, as the Pe was not scoreable at each site for some participants. There was a significant main effect for Site [$F(3, 198) = 39.82, p < .001$] indicating that the Pe was maximal at Pz, followed by Cz, FCz, and Fz across all participants. There were no group differences in the Pe (see Figure 2.1).

The Pe: Go/no-go task. An identical ANOVA was performed and revealed a significant a significant main effect for Site [$F(3, 207) = 58.96, p < .001$] such that the Pe was maximal at Pz, followed Cz, FCz and Fz across all participants. Again, there were no group differences in the Pe (see Figure 2.2).

The CRN: Flanker task. Figure 2.3 displays the averaged response-locked ERP waveforms during incongruent correct trials at each site for 15- and 18-year-olds. We scored the CRN as a deviation from the P3 peak to score the CRN (see for example, Santesso et al., in press; Scheffers & Coles, 2000). A Site by Group ANOVA produced a significant main effect for Site [$F(3, 213) = 12.0, p < .001$], with the CRN maximal at Cz, followed by FCz, Pz and Fz. No other significant main effects or interactions were found, indicating no age-related differences in the CRN. An identical ANOVA performed with the CRN measured as the peak deviation from the early baseline replicated these results.

The CRN: Go/no-go task. Figure 2.4 displays the averaged response-locked ERP waveforms during correct go trials at FCz for 15- and 18-year-olds. The CRN was indiscernible for many participants at Pz so we restricted this analysis to Fz, FCz, Cz. A Site by

Group ANOVA produced a significant main effect for Site [$F(2, 78) = 14.6, p < .001$], indicating that across participants the CRN was maximal at Fz, followed by FCz, and FCz with no group differences.

Analyses with CRN and ERN. In order to compare whether the variance associated with the CRN was the same as the variance associated with the ERN, we conducted a hierarchical regression analyses with the peak-to-peak ERN as the criterion variable, entering the peak-to-peak CRN on the first step, and group on the second step. The group effect remained significant at Cz [$F(2, 67) = 5.68, p < .01$] and at FCz [$F(2, 63) = 4.4, p = .02$]. A similar result at FCz was found with the go/no-go task [$F(2, 33) = 3.5, p = .04$].

Discussion

In the present study, we examined error-related ERPs in a large sample of healthy 15- and 18-year-old males using two tasks differing in difficulty and task demands. For the visual flanker task, we found no age-related differences in accuracy, response time, RT variability or post-error slowing. Therefore, any differences in the ERN were not due to differences in task performance or response control but were due to differences in the response monitoring system, i.e., in how individuals responded to their errors. We found that the ERN was smaller for 15- than for 18-year-olds but there were no group differences in the Pe or CRN. This is consistent with previous reports that also used a visual flanker task (e.g., Davies et al., 2004; Ladouceur et al., 2004). However, this is inconsistent with the results reported by Hogan and colleagues who examined ERNs in adolescents and young adults. These authors used a simple two-choice response task that yielded no differences in either performance or ERN amplitude between age groups. While we agree with these authors that the basic neural components of the response monitoring system are in place by the adolescent years, our findings suggest that they are not yet fully mature by 15 years of age, which may be due to structural or neurochemical immaturity. Not only did Hogan and colleagues use very small sample sizes, but also the age ranges examined were very broad: there were 12 adolescents between 12 and 19 years of age while there were 11 adults between 19 and 21 years. This may have precluded observation of subtle age differences between younger and older adolescents and also reduced the statistical power of the comparison. Davies, Segalowitz and Gavin (2004) noted that in their data the ERN increased dramatically in amplitude from 15-16 years to 17-18-years of age in males (with a more gradual increase in females), so using a narrower age range to represent *one* stage of adolescence (as we have done here) would be more likely to capture this change. The data reported by Davies et al., however, were based on 5 and 6 male participants in each group. The results of the present study therefore provide strong support for maturation of error monitoring from mid- to late adolescence.

We also found that the ERN was smaller for 15- than for 18-year-olds for the go/no-go task with no group differences in the Pe. Although the flanker task and go/no-go task involve overriding a prepotent response, the percentage of errors made on the go/no-go task was higher than on the flanker task over all participants confirming that this task was more difficult. We also found that 15-year-olds made significantly more errors than the 18-year olds on this task but showed similar response times and RT variability. Age-related differences in the ERN need not be attributed to poor performance (i.e., low accuracy). First, age-related differences in the ERN were found on the flanker task despite comparable performance. Second, as Pailing and Segalowitz (2004b) showed in young adults, increased task difficulty resulting in more errors does not affect the amplitude of the ERN, unless there is also increased uncertainty.

This suggests that under conditions of increased task demands, response monitoring in adolescents may be less efficient at the behavioral and neural level whereas for simple response tasks, differences may occur at the neural level only. Unlike Hogan and colleagues, however, we did not measure other indices of behavioral adjustment such as error correction, which may alter the otherwise spontaneous reaction to erroneous performance, and post-error slowing, which is not possible in our go/no-go task[3].

The present study found no age-related differences in the Pe in either task. This is consistent with previous developmental reports (e.g., Davies et al., 2004; Ladouceur, et al., 2004; Santesso, et al., in press) and suggests that the ERN and Pe may be functionally distinct from the ERN. Falkenstein and colleagues argued that the Pe might reflect conscious evaluation of an error as the Pe has been notably larger for perceived than unperceived errors (Falkenstein et al., 1991, 2000; Nieuwenhuis et al., 2001; Vidal et al., 2000). The absence of differences between groups in the Pe amplitude as well as in post-error slowing suggests that late response monitoring such as evaluation and adjustment strategies may be comparable in middle and late adolescents.

Finally, we found no group differences in the CRN. This suggests that 15-year-olds were no less certain of their performance than 18-year-olds on the correct trials. The ERN was also larger than the CRN for the flanker and go/no-go tasks indicating that both age groups were able differentiate correct and error trials. Importantly, we examined whether differences found in the ERN were attributable to differences in the CRN (i.e., level of certainty), but found that age-related differences in the ERN remained significant once controlling for the CRN. This finding is also consistent with the hypothesis that these components may be functionally distinct (Hajcak et al., 2003).

The data presented here add to the extant literature supporting late physiological or functional maturation of the ACC and attenuation of its error signals in the younger brain, for males at least. The 15- and 18-year-olds were similar with respect to correlates of response monitoring such as response time, error recognition (Pe), and post-response behavioral adjustment, but different in error monitoring (ERN) on both a simple and more difficult task. The growth of dopamine inputs to the prefrontal cortex during adolescence represents one of the neuronal mechanisms that increases the capacity for more mature judgment and inhibitory control (Lambe et al., 2000). Dopaminergic changes may have profound effects on behavior by altering the incentive value assigned to stimuli and the ability to simultaneously process information about antecedents and outcomes (and their emotional significance). These changes, in turn, may lead to the increased need to seek out novel, risky activities and make decisions on the basis of immediate reward. For example, both human and animal adolescents display higher preference for novelty, increased interaction with peers and risk-taking behaviors than individuals in any other age group (Arnett, 1999; Stansfield & Kirstein, 2006). A large body of animal work suggests that this "predisposition" toward novelty/risk may reflect dopaminergic changes occurring in the reward circuitry of the brain, including regions of the PFC (orbitofrontal cortex, medial PFC), limbic areas (see Spear, 2000 for review), and the transitional cortex between (ACC). Teicher and colleagues have even suggested that there is a shift in the balance toward greater predominance of dopamine activity in the PFC over the ACC in early adolescence that might partially account for differences in the reinforcing properties of stimuli observed in adolescents versus adults (Anderson, Dumont, & Teicher, 1997; Teicher et al., 1993). Our results support attenuation of the error signals in adolescents which may reflect the reduction of dopaminergic activity in this region.

Limitations of the present study include restricting the sample to 15- and 18-year-old males, precluding the examination of sex differences in the ERN as noted by Davies et al. (2004) and a detailed analysis of possible pubertal effects on performance monitoring. During the onset of and throughout the course of adolescence, there are significant changes in the hormone systems affecting both dopaminergic and cortical activity (Kritzer & Kohoma, 1998; Piazza & Le Moal, 1996). Future studies should aim to examine age- and sex-related differences in error-related ERPs to chart more accurately maturation of error monitoring and the ACC. This may be particularly useful in understanding reinforcement learning and the initiation of drug abuse, affiliation with antisocial peers and increases in impulsive/risk-taking behaviors, and differences observed between males and females.

Another issue is that the participants examined in the present study were recruited from different communities. Older adolescents were recruited from a university campus and a majority of the students had completed their first year of studies. In contrast, younger adolescents were recruited from the surrounding community from a variety of secondary schools. This may have resulted in group differences in intelligence and socio-economic status which were not controlled for in the present study. There is no evidence to date, however, that these factors affect the error monitoring process and error-related ERPs.

Future studies should also examine age-related changes in ACC activity using a variety of ERP tasks (e.g., gambling, decision-making) to determine how immaturity of this region (and other regions recruited by the ACC) contributes to more complex performance. How well the ACC initiates a cascade of events in which responses are evaluated and post-response adaptation of behavior occurs may be important for understanding reinforcement learning, maladaptive social behaviors, and one's propensity to engage in and evaluate risky events throughout development.

Chapter III: Performance monitoring and the propensity to take risks in males during late adolescence

Risk-taking has been associated with positive expectancies from engaging in risky behavior, sensation seeking and reward proneness, which may be linked with dopaminergic activity and poor reinforcement learning. The present study examined the relations between the propensity to engage in risky behaviors and three event-related potential (ERP) components related to error monitoring during a flanker task: the error-related negativity (ERN), error positivity (Pe), and the correct-related negativity (CRN). We found that higher scores on risk-taking, positive outcome expectancies for engaging in risks, sensation seeking and sensitivity to reward were related to smaller ERN amplitudes. These risk propensity measures were unrelated to the Pe and CRN and were also unrelated to risk propensity and behavioral measures of response time, accuracy and post-error slowing. Thus, high and low risk-takers do not differ in performance competency, response to errors (Pe), the certainty of having erred (CRN), and behavioral post-error adjustment. The present study provides support that risk-taking is related to poor error monitoring (ERN), specifically, a function of the dorsal anterior cingulate (ACC). Such poor ACC function may contribute to the desire to engage in risky behaviors for their rewarding properties without being deterred by potential negative outcomes.

Introduction

Risk-taking has been traditionally viewed as a personality trait based on the notion that some people are prone to take physical, financial, sexual and social risks because of some underlying difference in risk-seeking propensity (e.g., Blos, 1967; Freud, 1958; Jessor, 1983). Risk-taking behaviors occur frequently during adolescence, but perhaps even more so during the years 18-25 (Arnett, 1991; 1996; Byrnes et al., 1999; Greene, Kremar, Walters, Rubin, & Hale, 2000) with men engaging more than women in both risky (e.g., sports, drug use) and reckless (e.g., driving, sex) behavior (Bradley & Wildman, 2002; Gullone, Moore, Moss, & Boyd, 2000).

Risk-taking is highly correlated with sensation seeking or novelty seeking (i.e., the seeking of new and intense experiences and the willingness to take risks; Cloninger, Svrakic, & Przybeck, 1993; Zuckerman, 1994; Zuckerman & Cloninger, 1996). Several animal studies have demonstrated the rewarding effects of novelty (see Bevins, 2001; Bevins & Bardo, 1999; Besheer, Jensen, & Bevins, 1999). Accordingly, risk-takers may be strongly driven by reward (e.g., relaxation, exhilaration, pleasure) and engage in behaviors without proper regard for the consequences or risks involved, rather than being deterred by potential negative outcomes and/or punishment (e.g., arrest, bodily harm; Cloninger et al., 1993; Moore & Gullone, 1996; Zuckerman, 1994; Zuckerman & Kuhlman, 2000). In support for this hypothesis, several studies have reported that adolescents and young adults generated hedonic rationales and positive outcome expectancies for engaging in risky behaviors as well as a lack of deliberation (Fischer & Smith, 2004; Lavery & Siegel, 1993; Moore & Gullone, 1996; Santesso, Schmidt, & Fox, 2004; Parsons, Siegel, & Cousins, 1997)

A biochemical model of risk-taking holds that this trait is positively associated with the density of the dopamine transporter responsible for the presynaptic reuptake of dopamine, such that higher levels of risk or novelty seeking is related to reduced dopamine availability in the synaptic cleft and compensatory increased sensitivity of postsynaptic dopamine receptors (e.g., Cloninger, 1987; Ruegg et al., 1997). Two independent laboratories have provided evidence that novelty seeking in humans was positively associated with dopamine D_2 postsynaptic receptor sensitivity and with decreased presynaptic dopamine secretion and/or low dopaminergic activity (Gerra, et al., 2000; Hansenne et al., 2002).

To date, there have been few studies examining the neural correlates of risk-taking behavior. Rather, research has been primarily directed toward risky decision-making (i.e., making choices that yield high immediate gains in spite of higher future losses) and sensitivity to reward. Neuroimaging studies have demonstrated that risky decision- making on gambling tasks is associated with activity in the orbitofrontal, ventromedial and dorsolateral prefrontal cortices, the anterior cingulate cortex (ACC) and other regions (Adinoff et al., 2003; Ernst, et al., 2002; Fellows & Farah, 2003). Event-related potential (ERP) studies investigating the response to feedback during gambling tasks have shown that negative feedback (e.g., monetary loss) elicits a larger error-related negativity (ERN; see below) component than positive feedback (e.g., Gehring & Willoughby, 2002; Yeung & Sanfey, 2004), consistent with its hypothesized generation in the ACC and its association with complex decision-making and the resolution of conflicting information processing. The ACC is central to a network critical to performance monitoring involving the detection and emotional appraisal of correct and error responses, as well as post-response adjustment. This process appears to activate the ACC, which subsequently generates three characteristic response-locked ERPs: the ERN, Pe and CRN.

Performance monitoring and error-related ERPs

The ERN. The ERN appears as a negative deflection in the ERP waveform peaking approximately 50-100 ms following error responses. The ERN has a fronto-central scalp distribution and source localization studies suggest that the ERN is generated by the dorsal ACC (Dehaene, Posner, & Tucker, 1994; Falkenstein, Hoorman, Hohnsbein, & Blanke 1991; Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002). There appears to be mounting evidence supporting a biochemical model of the ERN (e.g., de Bruijn, Hulstijn, Verkes, Ruigt, & Sabbe, 2004; Zirnheld et al., 2004). Holroyd and Coles (2002) proposed the ERN reflects modulation in ACC activity caused by phasic decreases in dopaminergic activity following error responses. This error/negative reinforcement learning signal is used by the ACC to adjust the cognitive system and performance on the task at hand. Consistent with the view that the ERN reflects a reinforcement signal that modulates subsequent response selection, Frank and his colleagues reported that the amplitude of the ERN predicted the degree to which individuals learned about the negative consequences (e.g., errors) of their actions (as opposed to the positive; Frank, Woroch, Curran, 2005). That is, larger ERNs were associated with a bias to learn to avoid negative events.

The functional significance of the ERN is still a matter of debate. Earlier accounts held that the ERN reflects the activity of a general response monitoring system that detects errors by signalling a mismatch between an intended and observed response (Bernstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991). Others have argued that the ERN reflects conflict arising from the coactivation of both correct and error response channels (Carter et al., 1998). Most recently, Botvinick, Cohen and Carter (2004) attempted to reconcile these theories and the dissociations found between response conflict and ERN amplitude changes (e.g., Christ, Falkenstein, Heuer, & Hohnsbein, 2000; Luu Flaisch, & Tucker, 2000; Masaki & Segalowitz, 2004; Pailing & Segalowtiz, 2004a) and suggested that conflict might constitute one part of the more generic monitoring system.

Rather than viewing the ERN as only a cognitive and/or motor process, research is now being directed toward examining the emotional appraisal of errors and the influence of affect and motivation on the ERN amplitude, as this may provide insight into adaptive, goal-directed behaviors. Early research demonstrated that the experience of negative affect, concern over the outcome of an event, and excessive self-monitoring (e.g., obsessive-compulsive disorder) were associated with larger ERNs (Gehring, et al., 2000; Johannes, et al., 2001; Luu, Collins, & Tucker, 2000). In contrast, diminished ERNs have been related to a lack of concern over the outcome of an event. For example, Dikman and Allen (2000) reported individuals scoring low on a measure of socialization (e.g., stealing, inhibition, and responses to reward) displayed smaller ERNs during incorrect avoidance learning trials. Pailing and Segalowitz (2004b) reported that the ERN varied with motivational level, particularly for individuals with low conscientiousness scores (i.e., low on cautiousness, deliberation, dependability, persistence, and meticulousness; Costa & McCrae, 1992). Taken together, results suggest that the size of the ERN may reflect concern over the outcome of an event, monitoring vigilance and/or error saliency.

The Pe. The Pe is a late positive component peaking 200-500 ms after an error response. Whereas the ERN has been localized to the caudal ACC, the Pe may be generated by the rostral ACC and superior parietal cortex (Herrmann et al., 2004; Van Veen & Carter, 2002a). There is also some functional distinction between the ERN and Pe, with the Pe reflecting conscious evaluation of an error after overt error responses (Falkenstein et al., 1991, 2000; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Vidal et al., 2000) and is not influenced by stimulus compatibility, expectancy factors (Bartholow et al., 2005) or sleepiness (Murphy, Richard, Masaki, & Segalowitz, 2006) whereas the ERN is.

Research investigating the relation between affective style and the Pe is inconclusive. As Falkenstein and others suggest, greater awareness of and emotional or cognitive reactions to the appropriateness of a response may be reflected by a larger Pe (Falkenstein et al., 1991, 2000). Consistent with this hypothesis, we demonstrated that obsessive-compulsive tendencies were associated with a larger Pe in children (Santesso, Segalowitz, & Schmidt, 2006). This finding has not been replicated, however, in obsessive-compulsive adult patients (Ruchsow et al., 2005). In another report, Eysenck's personality factors (Neuroticism, Extraversion, Psychoticism) were unrelated to Pe amplitude in children (Santesso, Segalowitz & Schmidt, 2005). Taken together, these findings suggest that the Pe may be less influenced by affective traits (e.g., anxiety, sociability) than the ERN and more by the person's state.

The CRN. The correct-related negativity (CRN) is a negative deflection occurring on correct trials within the same time-window of the ERN and has similar morphological and topographical properties as the ERN (Vidal et al., 2000). Prevailing theories view the CRN as an index of uncertainty about the correctness of a response (Scheffers and Coles, 2000) as the CRN and ERN become more similar to each other in magnitude when task difficulty and subjective ratings of uncertainty increase (Hogan, Vargha-Khadem, Kirkham, & Baldeweg, 2005; Pailing and Segalowitz, 2004a). This may be simply because when uncertainty about performance increases, the averaged ERP to correct trials is contaminated by trials which were coded as errors. Indeed, correct responses that are preceded by initiating and halting a wrong response are associated with large ERNs, although not as large as are associated with complete errors (Masaki & Segalowitz, 2004; Vidal, 2000).

Affective and motivational influences on the CRN have also been inconclusive. For example, Hajcak and his colleagues (2003) reported that the CRN and ERN were enhanced in young adults scoring high on a measure of worry, suggesting similarity between the two components. However, this same group of researchers reported that the amplitude of the CRN was not influenced by more valuable errors and under conditions of performance evaluation (Hajcak, Mosner, Yeung & Simons, 2005). A difficulty in interpreting the CRN is that we don't know for any particular participant how many correct trials are coded as errors.

The present study

While most of the previous work on personality and the ERN have focused on negative affective traits and psychopathology, the contribution of performance monitoring to risk-taking is also important. This is especially the case for adolescents and young adults who frequently experiment with a wide range of novel, risky activities. While some degree of adolescent risk-taking is both statistically normative and psychologically adaptive (e.g., Hurrelmann, 1990; Shedler & Block, 1990), some forms of risk-taking are maladaptive and risk-takers may experience problems as a result of their behaivors. Risk-taking may lead to negative outcomes such as substance dependence (Robins & Przybeck, 1985), academic failure (Kaplan & Liu, 1994; Newcomb & Bentler, 1988) and impairments in memory and attention (see Brown & Tarpet, 2004 for review). Despite the sometimes transient nature of risk-taking behavior (i.e., such behaviors decline in the late 20's; Statistics Canada, 2004), Moffit (1993) argued that individuals may become "ensnared by the consequences" of delinquent behavior. For example, adolescents may fail to develop a repertoire of prosocial behavior and miss opportunities to affiliate with prosocial peers and, instead, build a bad reputation, poor academic/work history and possibly a criminal record that would limit opportunities for success later on.

The goal of the present study was therefore to examine error-related ERPs in relation to four self-report measures of risk-taking propensity: risk-taking, positive outcome expectancies, sensation seeking and sensitivity to reward. We tested late adolescent males between the ages of 18 to 19 years because risk tendencies occur most frequently during this period, especially in men (Arnett, 1991, 1996; Bradley & Wildman, 2002; Byrnes et al., 1999; Greene et al., 2000; Gullone et al., 2000). Given the nature of risk-taking and sensation seeking and their relation to dopamine and prefrontal activation, we expected that high risk-takers might exhibit poorer error monitoring than low risk-takers. That is, high risk-takers may monitor their performance less vigilantly and be less concerned over the outcome of their responses. Additionally, high risk-takers may not show a bias to avoid negative events (e.g., errors) reflecting possible deficits in reinforcement learning (Frank et al., 2005). We hypothesized that high risk-takers will therefore exhibit smaller ERNs than low risk-takers. Since the Pe and CRN are less sensitive to affect and/or motivation, we predicted that there would be no difference in these ERP components in high and low risk-takers. Fundamental to these predictions is the expectation that high risk-takers would show comparable recognition and/or awareness of errors and would be no less certain about their responses.

Method

Participants

Data from 38 late adolescent males between the ages of 18 to 19 years (M = 18.50, SD = .64) were recruited from Brock University. The majority of participants were Caucasian and right-handed. Each participant received $10 per hour for his participation.

Electrophysiological tasks

Participants completed the flanker task described in Chapter I, page 7.

Electrophysiological recording and data reduction

All recording and data reduction procedures were identical to those described in Chapter I, page 8.

Behavioral Measurements

The behavioral measurements used for this study were identical to those described in Chapter I, page 11.

Dipole Source Localization

Data from all available electrodes were 1-30 Hz bandpass filtered. Dipole models were computed using BESA 5.1 for the error trial grand average waveform during the flanker task, with the epoch for the ERN being defined by the associated increase in global field power. For each solution two fixed, symmetrical regional source dipoles were placed around the eyes to capture the variance associated with eye movements (Talairach coordinates; $x = +/- 26.0$, $y = 65.8$, $z = -23.6$). Then, a four-dipole model was derived. Symmetry constraints with respect to location were applied to each free dipole pair. The reported dipole solutions were stable across different starting positions.

Self-report measures

Cognitive Appraisal of Risky Events (CARE). Risk-taking was assessed using 25 items from the CARE Frequency of Involvement Scale (Fromme, Katz, & Rivet, 1997). The CARE Frequency of Involvement Scale assesses different types of risk-taking behaviors: aggressive and illegal behaviors, risky sexual activities, heavy drinking, illicit drug use, and high-risk sports. Participants were asked to indicate the frequency in which individuals have engaged in 25 risk behaviors over the past 6 months ranging from 0 (never) to 4 (10 or more times). The CARE questionnaire also measures positive and negative outcome expectancies – the likelihood of negative (risk) and positive (benefit) outcomes of engaging in the 25 risky behaviors. Participants used a 6-point Likert scale raging from 0 (not at all likely) to 5 (extremely likely). Alpha coefficients for the CARE questionnaire range from .68 to .85.

Sensation Seeking Scale Form-V (SSS-V). Sensation seeking was assessed using 40 items from the SSS-V (Zuckerman, 1994). This scale is designed to measure four factors of sensation seeking (10 items each): thrill and adventure seeking, experience seeking, disinhibition, and boredom susceptibility. Thrill and adventure seeking comprises the desire to engage in physically risky activities such as risky sports; experience seeking comprises the need to seek experience through the mind and sense, as accomplished though music or art; disinhibition comprises the desire to seek social stimulation in uninhibited social activities, such as parties; and boredom susceptibility comprises an aversion to monotony and preference for the unpredictable (Kopstein, Crum, Celentano, & Martin, 2001). Participants are asked to indicate whether a given statement accurately describes them. Internal reliability of this scale ranges from .83 to .86.

Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ). The SPSRQ (Torrubia, Avila, Molto, & Caseras, 2001) is a 48-item questionnaire designed to assess worrying about threats of punishment or failure, behavioral inhibition, impulsivity, and the extent to which individual do things to obtain rewards. Participants are asked to indicate by circling 'Yes' or 'No' whether a given statement accurately describes them. The alpha coefficients for males are .83 for sensitivity to punishment and .78 for sensitivity to reward.

Results

Behavioral data

Table 3.1 presents the means (SD) for response time (RT), accuracy and post-error slowing across participants during the flanker task. In order to analyze response time, we performed an ANOVA with Category (Congruent, Incongruent) and Response (Correct, Error) as within-subjects factors. There was a significant main effect for Category [$F(1, 36) = 10.7, p < .01$] and Response [$F(1, 36) = 61.7, p < .001$] indicating that RTs were faster for congruent compared with incongruent trials and for errors compared with correct responses. We also found that participants committed significantly higher percentage of errors on incongruent compared with congruent trials [$F(1, 36) = 19.9, p < .001$]. Finally, we examined post-error slowing on incongruent trials using an ANOVA with Category (Correct after correct RT, Correct after error RT) as the within-subjects factor. Participants showed post-error slowing such that RTs were slower following errors than following correct responses [$F(1, 36) = 6.7, p = .01$].

We performed a series of Pearson correlations to examine the relations between the data on incongruent trials and the personality measures. There were no significant relations between personality and mean response time (and standard deviation of RT), accuracy or post-error slowing.

Personality in relation to error-related ERPs

Table 3.2 presents the means (SD) for the ERN, Pe and CRN amplitudes. An ANOVA with Site (Fz, FCz, Cz, Pz) indicated that the ERN was maximal at FCz followed by Cz, Fz and Pz [$F(3, 408) = 35.5, p < .001$]. A similar ANOVA showed the Pe was maximal at Pz followed by Cz, FCz and Fz [$F(3, 111) = 17.9, p < .001$]. The CRN was maximal at FCz follwed by Cz, Pz and Fz, but the difference between sites was not significant. Finally, the positive peak preceding the ERN (i.e., the P3) was maximal at Pz followed by Cz, FCz and Fz [$F(3, 108) = 11.69, p < .001$].

We performed a series of Pearson correlations to examine the relations among the error-related components (ERN, Pe, CRN) and our personality measures (see Table 3.3). First, we found that Risk-taking was positively related to Sensation Seeking ($r = .54, p < .001$), Sensitivity to reward ($r = .37, p = .02$) and Positive outcome expectancies ($r = .38, p = .02$). Sensation seeking and Sensitivity to reward were also highly related ($r = .42, p < .01$) but neither of these measures was related to Positive outcome expectancies. Sensitivity to punishment and Negative outcome expectancies were not related to any of the personality measures. Second, as can be seen in the scatter plots (Figure 3.1 A-D), high risk-taking scores were associated with smaller ERNs at Cz, $r = .43, p < .01$. A similar relation for the ERN at Cz was found for Sensation seeking ($r = .44, p < .01$), Sensitivity to reward ($r = .38, p < .01$) and Positive outcome expectancies ($r = .33, p = .05$). The associations between the ERN and Sensitivity to punishment or Negative outcome expectancies were not significant. Identical results were found when we examined the peak-to-peak ERN in relation to these measures. To ensure that variability related to the P3 preceding the ERN was not contributing the present findings, we ran two additional analyses. First, we performed a Pearson correlation between the P3 and the measures of personality and found no significant relations. Second, we calculated ERN amplitude partialing out the variability due to the P3 using a regression method. In this regression, the ERN amplitude at Cz served as the criterion variable, the P3 amplitude was entered as the predictor and the residual values were saved. We found that these significant relations remained using the residualized ERN. There was no significant associations between the Pe or CRN with Risk-taking, Sensation seeking or Sensitivity to reward (or Sensitivity to punishment).

Given that there were significant inter-correlations among Risk-taking, Sensation seeking, Sensitivity to reward and the ERN, we performed a multiple regression analysis to determine which of these personality variables accounted for the most variance in the ERN amplitude. ERN amplitude at Cz served as the criterion, and we entered Risk-taking, Sensitivity to reward and Sensation seeking simultaneously as the predictors (see Table 3.4). None of these variables accounted for a significant amount of unique variance: Risk-taking accounted for 3.8%, Sensation seeking less than 3.3%, and Sensitivity to reward 3.1%, totalling 27.5% of variance in ERN amplitude when the overlap is included as well.[4] Because of this high overlap among the predictors, we formed a composite measure of "risk propensity" by z-scoring and averaging the scores. A Pearson correlation revealed a stronger association to the ERN using this composite measure such that high risk propensity was related to significantly smaller ERNs at Cz ($r = .52$, $p = .001$). To illustrate the relation between risk propensity and the ERN, we formed two groups based on a median split of the composite scores: a high ($M = 1.91$, $SD = .32$, n = 19) and a low ($M = -2.06$, $SD = .26$, n = 19) risk propensity group. Independent t-tests confirmed, as predicted, that individuals with high risk propensities had a smaller ERN at Cz compared with the low group, $t(36) = 2.67$, $p = .01$ (see Figure 3.2). This difference remained when analyzing the peak-to-peak and the residualized ERN between groups. Note the P3 was also unrelated to the composite measure of risk propensity. There were no significant group differences in response time (means or standard deviations), accuracy or post-error slowing, precluding these factors from being potential confounds.

Dipole source localization

We examined the neural source generating the ERN by creating a dipole solution using a 50 ms time window around the ERN peak which occurred at 80.0 ms (i.e., 52-112 ms window). Figures 3.3 displays the dipole solution for the ERN during the flanker task for all participants. A good model (RV = 3.44%, best = 2.17%) was obtained. In addition to the symmetrical ERN dipoles located in the dorsal portion of the ACC (Lancaster, Woldorff et al., 2000; BA 24, Talairach coordinates, x = +/- 7.0 y = 0.3, z = 46.1) which accounted for the negativity at the fronto-central sites, this model included a symmetrical dipole pair located in the region of the parahippocampus (BA 30, x = +/- 22.0, y = - 50.1, z = 3.5).

Discussion

The purpose of the present study was to examine the relation between electrophysiological correlates of performance monitoring and risk-taking propensities. We measured risk-taking propensity in late adolescent males aged 18-19 years using a measure of risk-taking frequency, outcome expectancies, sensation seeking, sensitivity to reward and punishment. We found no relations between the performance measures on the flanker task and personality or error-related ERP components. Therefore, it can be argued that any differences in the error-related ERPs were not due to differences in task performance but were due to differences in the response monitoring system in reward-seeking individuals. We found that smaller ERNs at the central site were associated with higher scores on risk-taking, positive outcome expectancies, sensation seeking and sensitivity to reward. None of these risk-propensity measures were related to the Pe or CRN. Consistent with previous reports, dipole source localization located the ERN in the dorsal ACC.

Individuals with a propensity to take risks exhibited smaller ERNs during a simple visual discrimination task. These ERN results are consistent with the view that the ERN does not simply reflect a cognitive or motor process, but is sensitive to affective responses to errors and goal states (such as reward seeking). We not only measured underlying propensities to take risks (sensation seeking, reward sensitivity) but also behavioral outcomes (risk frequency) and cognitions and/or attitudes towards risk-taking (outcome expectancy). There was substantial overlap among these measures in predicting the ERN, which suggests that the ERN may reflect activity of a very basic system that integrates information at multiple levels, both emotional and cognitive. A likely interpretation is that the ERN reflects a dopaminergic reinforcement learning signal (Holroyd & Coles, 2002). Individuals with high risk propensities may be driven to seek novel, rewarding experiences (and perceive positive outcomes from engaging in such experiences) and, when unfavorable outcomes are encountered, show diminished responsiveness to threat and/or errors and are less likely to learn from past negative experiences.

Such a response has, of course, an affective component (e.g., not caring about errors), rather than only a biochemical and learning side (e.g., dopaminergic and reinforcement learning dysfunction). Our findings are indeed consistent with two other reports supporting affective relations with the ERN. First, to the extent that our measure of risk propensity reflects lack of deliberation, the present study is consistent with Pailing and Segalowitz (2004a) who reported that larger motivational manipulation of the ERN were associated with lower conscientiousness scores (including deliberation, cautiousness). The authors argued that individuals scoring low on conscientiousness were sensitive to manipulations that alter the salience of errors. Second, similar to Dikman and Allen (2000), our measures tapped inhibition and reward responsivity. These authors reported that socialization (including inhibition, responses to reward) was related to the ERN such that low-socialized participants generated smaller ERNs during incorrect avoidance learning trials than during incorrect reward trials compared with high-socialized individuals. It may be the case that our high risk-seeking participants were less motivated on the task and less concerned with the outcome of their responses. Alternatively, a biological predisposition (e.g., dopamine activity) and affective indifference may have contributed to these participants' poor error monitoring. Unfortunately, the present study used a standard flanker task that precluded the examination of motivational influences on high and low risk-taking individuals. Future studies should examine the ERN using paradigms that alter the emotional significance of errors (e.g., feedback ERNs) and perhaps examine biochemical correlates of the ERN and risk-taking behaviors.

We found that the Pe and CRN were unrelated to risk propensities. Falkenstein and colleagues argued that the Pe might reflect conscious evaluation/recognition of an error as the Pe has been notably larger for perceived than unperceived errors (Falkenstein et al., 1991, 2000; Nieuwenhuis et al., 2001; Vidal et al., 2000). The absence of associations between the Pe, post-error slowing and the personality measures suggests that late response monitoring such as error evaluation and post-error adjustment do not differ between high and low risk prone individuals. Additionally, there were no associations between the CRN and the personality measures, which suggests that individuals high on measures of risk propensity were no less certain of their performance than those low on this measure. Taken together, these results suggest that there is some functional dissociation between the ERN and the Pe and CRN such that the latter two components are not influenced by traits we measured whereas the ERN is.

Although poor error monitoring was related to the risk propensities, there might be other important factors not examined here that predispose individuals to engage in risky activities. Physiologically, the tendency to take risks may be hormonally driven (e.g., testosterone; Daitzman, Zuckerman, Sammelwitz, & Ganjam, 1978; Daitzman, & Zuckerman, 1980; Gerra et al., 1999) and/or a consequence of central nervous system under-arousal as indexed by lower resting heart rate (Ridgeway & Hare, 1981; Robinson & Zahn, 1983) and low basal cortisol levels (Netter, Henning, & Roed, 1996; Wang, et al., 1997). Risk-taking may thus represent a form of external stimulation facilitating optimal levels of arousal (Zuckerman, 1990). Risk-taking may also be influenced by social factors such as peer influences (e.g., peer risk-taking, peer pressure; e.g., Bauman & Ennett, 1994). Each of these research areas is important to examine alongside performance monitoring in order to obtain a fuller picture of the antecedents of risk propensity and possible additive effects of these factors in risk-taking outcomes.

The present study had several limitations. First, although we chose to examine male participants because risk-taking behaviors occur more frequently in males than in females, studies examining error monitoring and risk-propensity in both males and females are needed before generalizations can be made. Importantly, gonadal hormones may influence dopamine activity, and consequently error-related ERPs. For example, androgens and estrogens are powerful regulators of dopaminergic (and serotoninergic) afferents innervating the prefrontal cortex (Kritzer & Kohoma, 1998; Handa, Henja, & Lorens, 1997) while progesterone may decrease brain excitability (Holzbauer, 1976) and have an inhibitory effect on cognition (e.g., Sherwin, 1988). These results suggest that individual differences in risk and sensation seeking (which may be linked to underlying hormone levels) may influence error monitoring differently in men and women. Second, we examined error monitoring in males between the ages of 18-19 years, whereas risk-taking behaviors begin to emerge early in adolescence, reach maximal levels in the mid-20s and begin to decline thereafter. This well-documented trend suggests that there may be developmental changes in the ACC (Segalowitz & Davies, 2004) but also changes in reward sensitivity (e.g., May et al., 2004) contributing to error monitoring and risk-taking tendencies across the lifespan. Future studies should therefore be directed towards age-related changes in error monitoring in relation to reward processing and risk-taking behaviors in both males and females. Third, the risk-taking and sensation seeking scores obtained in the present study were not extremes. Accordingly, the high risk-takers reported here might not be representative of those individuals who approach clinical categories. The extreme ends are perhaps more representative of the people who engage in maladaptive forms of risk and reward seeking than the young males presented here. Finally, the present study used a visual flanker task to elicit errors. It might be more informative, however, to examine whether the ERN predicts the degree to which high and low risk seeking individuals learn about the negative consequences of their actions (Frank et al., 2005) as well as how these individuals respond to negative feedback. Future studies should include reinforcement learning paradigms and examine feedback ERNs and other feedback components (e.g., P3) as these may be sensitive to reward valence and magnitude (e.g., Yeung & Sanfey, 2004).

Summary

In summary, the present study provides support for the view that the ERN is sensitive to affective traits, specifically, the propensity to engage in risky activities. This relation was not found for the Pe and CRN, which suggests that there is functional dissociation between the components and high risk-takers may show poor error monitoring as opposed to poor recognition, and decreased certainty of errors. The results of the present study have important implications for understanding how diminished responsiveness to unfavorable outcomes may be associated with risk-taking and other disinhibited behaviors. Diminished responsiveness to unfavorable outcomes may also be compounded by the fact that adolescents and young adults rarely experience the negative outcomes but experience the positive outcomes immediately when engaging in risky behaviors (Moore & Gullone, 1996). The present findings therefore add to the literature supporting the hypothesis that intervention programs aimed at deterring risky behaviors via threats of punishment may be ineffective. Rather, intervention programs should give emphasis to adaptive and rewarding alternatives to risky activities.

Chapter IV: Poor error monitoring response is related to lack of empathy in males

Empathy is a multidimensional construct involving sophisticated cognitive and affective processes. Several neural imaging studies have identified regions of prefrontal and medial frontal cortex (including anterior cingulate cortex, ACC) mediating empathic abilities but to date, no such electrophysiological studies exist. We examined cognitive and affective empathy in relation to error monitoring behaviorally and as reflected electrophysiologically in the error-related negativity (ERN) and error positivity (Pe) in 18- to 19-year-old males during two visual response tasks. We found that low scores on the empathy measure were related to small ERNs on both tasks, but were unrelated to the Pe. Results provide support for the role of the ACC in empathy and suggest that the ERN may be influenced by the extent of individuals' concern with the outcome of events. The present study may also provide insight into general reinforcement learning deficits contributing to the development of maladaptive social behaviors in individuals with low empathy.

Introduction

Empathy is an important aspect of effective social interaction that involves both sophisticated cognitive and affective processes. Contemporary accounts have emphasized how empathy is multidimensional. According to Baron-Cohen (2004), cognitive empathy refers to an observer understanding others' feelings and the ability to take their perspective (i.e., theory of mind). This process requires the observer to "set aside their own current perspective, attributing a mental state to the other person, and then inferring the likely content of their mental state" (p. 26). Affective empathy refers to an observer making an *appropriate* emotional response to another person's emotional state.

Baron-Cohen (2004) argued that spontaneous empathy is a defining feature of human relationships: "it stops an observer from doing things that would hurt another person's feelings, predict another person's behavior, and provides a framework for the development of a moral code" (p. 24). High empathic ability has been related to prosocial behaviour (e.g., helping) (Batson, 1991), whereas low empathic ability has been associated with self-centeredness, alienation of others and social conflict (Eslinger, Parkinson, & Shamay, 2002). It is not surprising that problems with empathy have been noted in conduct disordered youth and adults diagnosed with psychopathy (Frick & Ellis, 1999; Soderstrom, 2003). Several researchers have argued that psychopathic individuals lack appropriate affective reactions to another's affective state (i.e., a psychopath does not *care*) (Blair, Jones, Clark, & Smith, 1997; Mealey, 1995) and lack guilt or compassion in the presence of another's distress, which are fundamental features of empathy (Checkley, 1977; Hare et al., 1990). Given these associations, it may be of particular interest for psychologists to investigate the neural correlates of empathy as this might provide insight into the development and/or maintenance of abnormal social behavior.

Neural correlates of empathy. Considering the multifaceted nature of empathy, it is only likely that a complex neural network mediates it. Neuroimaging studies have identified various neural systems, most notably regions within the prefrontal cortex (PFC), underlying cognitive and affective empathy. In an early study, Grattan and colleagues examined cognitive empathy in adults with PFC and parietal cortex (PC) lesions, with the greatest impairment in patients whose PFC lesion was restricted to the orbiofrontal cortex (OFC) (Grattan, Bloomer, Archambault, & Eslinger, 1994). More recently, Shamay-Tsoory and colleagues reported that self-reported cognitive empathy was impaired in patients with either right or left PFC lesions, or in patients with PC lesions confined to the right hemisphere. The most severe deficit emerged in patients with right ventromedial PFC lesions (Shamay-Tsoory, Tomer, Berger, Aharon-Peretz, 2003). In a second study, both cognitive and affective empathy were impaired following right or left PFC lesions or right PC lesions (Shamay-Tsoory, Tomer, Goldsher, Berger, & Aharon-Peretz, 2004).

The studies reported above assessed empathy using self-report trait measures. A more complicated story emerges, however, when assessing empathic decisions and empathy-related constructs such as theory of mind, sympathy, and the perception of pain in others. For example, Farrow et al. (2001) used fMRI to examine empathic judgements (i.e., another's state of mind) to pictorially presented scenarios. Empathic judgements in healthy adults activated left-sided regions including the superior frontal and lateral inferior frontal gyrus, middle temporal gyrus, anterior middle temporal gryus as well as the orbitofrontal gyrus. Vollm et al. (2006) investigated both empathy and theory of mind in healthy adults using comic strips depicting short stories. Both empathy and theory of mind activated medial prefrontal and temporal cortices and OFC. Theory of mind, however, specifically activated (mostly) right-sided OFC, middle frontal gyrus, and superior temporal gyrus whereas empathy activated the left amygdala, anterior and posterior cingulate and medial PFC.

Sympathy is one type of empathic response; rather than feeling the same emotion as the other person, it is characterized by both an emotional response to someone else's distress and a desire to alleviate the other person's suffering (Baron-Cohen, 2004; Decety & Chaminade, 2003). Decety and Chaminade (2003) recently examined the neural correlates of sympathy in healthy participants by presenting video clips showing actors telling sad and neutral stories. Compared with neutral stories, sad stories activated the right inferior parietal cortex, dorsal premotor and pre-supplementary motor area, all of which may be linked with "shared representation" of another individual's behavior. Similarly, Singer et al. (2004) examined activation while adults either experienced a painful stimulus or when they observed a signal indicating that their loved one experienced pain (i.e., empathy was induced). The authors reported that in both conditions there was activation in the bilateral anterior insula (AI), rostral anterior cingulate cortex (ACC), brainstem, and cerebellum. Furthermore, AI and ACC activation correlated with trait empathy scores.

The results of these neuroimaging studies implicate a strong role for the prefrontal (right- or left-sided) and medial prefrontal cortex in empathic ability. Although there have been no studies examining the electrophysiological correlates of empathy, the use of error-related ERPs may also provide important information about the neural generators of trait empathy as well as associated cognitive processes. One approach may be investigating performance monitoring (as indexed by ACC-generated ERPs) in relation to empathy. The ACC has anatomical connections to attentional, motoric and affective areas of the brain including the amygdala, PFC and OFC (see Devinsky, Morrell, & Vogt, 1995 for review). The detection and emotional appraisal of correct and error responses, as well as post-response adjustment, have been consistently linked to activity of this region (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; van Veen & Carter, 2002). Consequently, ACC activity may be indirectly measured by error-related ERPs: the error-related negativity (ERN) and error positivity (Pe).

The ERN. The ERN appears as a negative deflection in the ERP waveform peaking approximately 50-100 ms following error responses. The ERN has a fronto-central scalp distribution and may be generated by the caudal ACC (Dehaene, Posner, & Tucker, 1994; Falkenstein, Hoorman, Hohnsbein, & Blanke 1991; Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002). A biochemical model of the ERN proposes that there is a phasic decrease in dopaminergic activity following errors in the prediction of a future event (e.g., an error response). This error or negative reinforcement learning signal is conveyed to the ACC where the ERN is produced and subsequent response selections are modulated (Holroyd and Coles, 2002; Schultz, Dayan, & Montague, 1997). Frank and his colleagues recently found evidence that the ERN may reflect a negative reinforcement signal. In their study, larger ERNs were associated with a bias to learn to avoid negative events (more than to seek positive events) and thus predicted the degree to which individuals learned about the negative consequences (e.g., errors) of their actions (Frank, Woroch, Curran, 2005).

Early accounts proposed the ERN reflects the activity of a general response monitoring system that detects errors by signalling a mismatch between an intended and observed response (Bernstein, Scheffers, & Coles, 1995; Falkenstein et al., 1991). Others have argued that the ERN reflects conflict arising from the coactivation of both correct and error response channels on error trials (Carter et al., 1998). Most recently, Botvinick, Cohen and Carter (2004) suggested that conflict might constitute *one* instance of amore generic monitoring system.

Another line of research proposes that the ERN reflects the emotional appraisal of errors and affective goal states. On the one hand, the experience of negative affect, concern over the outcome of an event, and excessive self-monitoring (e.g., obsessive-compulsive disorder) may be associated with larger ERNs (Gehring, et al., 2000; Johannes, et al., 2001; Luu, Collins, & Tucker, 2000; Santesso, Segalowitz & Schmidt, 2006). On the other hand, a lack of concern over the outcome of an event (i.e., not *caring*) may be associated with smaller ERNs.

To date, there have been no studies directly examining the relation between empathy and the ERN but two independent groups of researchers have examined empathy-related constructs. For example, Dikman and Allen (2000) investigated the ERN in individuals scoring low on a measure of socialization, which may be considered a precursor of psychopathy and linked with lack of empathy (Gough, 1994; Hare et al., 1990). The authors reported that individuals scoring low on measures of socialization displayed smaller ERNs during incorrect avoidance learning trials. Pailing and Segalowitz (2004) later reported that the ERN varied with motivational level particularly for individuals with low conscientiousness scores. The authors suggested that individuals scoring low on conscientiousness are sensitive to manipulations that alter the salience or the significance of an error or, alternatively, highly conscientious individuals may have been less sensitive to the motivational manipulations because they were motivated to perform well regardless of external incentives (i.e., they always *care*). Importantly, low conscientiousness has been previously associated with lack of empathy (Jolliffe & Farrington, 2005). More recently, Santesso, Segalowitz, and Schmidt (2005) reported that children scoring high on measures of psychoticism and poor social behavior displayed smaller ERNs compared with children displaying good social behaviors. Again, psychoticism may be predictive of antisocial behaviors and psychopathology later in life (Eysenck, 1997; Lane, 1987; Romero et al., 2001). Taken together, these results suggest that the ERN may be influenced by the extent to which individuals care or, rather, care about the outcome of their behaviors. Moreover, diminished responsiveness to unfavorable outcomes may be indicative of general disinhibition and/or hypo-responsivity to unfavourable cues and/or poor reinforcement learning (e.g., Bechara, Dolan, & Damasio, 2002; Howland, Patterson, Kosson, & Newman, 1993; Newman, 1987).

The Pe. The Pe is a late positive component peaking 200-500 ms after an error response. Whereas the ERN has been localized to the caudal ACC, the Pe may be generated by the rostral ACC and superior parietal cortex (Herrmann et al., 2004; Van Veen & Carter, 2002). There is also some functional distinction between the ERN and Pe, with the Pe reflecting conscious recognition of an error or further cognitive/affective processing after error recognition (Falkenstein et al., 1991, Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Falkenstein, Willemssen, Hohnsbein, & Hielscher, 2005; Vidal et al., 2000) and is not influenced by stimulus compatibility or expectancy factors whereas the ERN is (Bartholow et al., 2005) while the Pe, but not the ERN, is affected by sleepiness (Murphy, Richard, Masaki, & Segalowitz, 2006). Additionally, the Pe may not be influenced by age and/or dopaminergic activity. For example, whereas age-related differences have been observed across childhood and adolescence (with the ERN increasing with age) no differences in the Pe have been observed (e.g., Davies, Segalowitz, & Gavin, 2004; Ladouceur, Dahl, & Carter, 2004; Santesso, Segalowitz, & Schmidt, in press). Falkenstein and his colleagues also found no differences in the Pe between adult Parkinson disease patients (characterized by dysfunction in the dopamine system) and controls, despite differences in the ERN (Falkenstein et al., 2005).

Some research has been directed toward understanding affective influences on the Pe, with little resolve, suggesting that the Pe may be less influenced by affective style (e.g., anxiety, sociability) than the ERN. For example, it has been observed that the Pe is unrelated to

OCD (Ruchsow et al., 2005) and risk/sensation seeking (Santesso & Segalowtiz, submitted) in adults, and poor social behaviors in children (Santesso et al., 2005).

The present study

The purpose of the present study was to examine electrocortical correlates of performance monitoring (as indexed by the ERN and Pe) as it relates to trait empathy in late adolescent males. This may provide insight into the degree to which individuals can learn, and care about the negative consequences (e.g., errors) of their actions (e.g., Frank et al., 2005). The participants studied here may be particularly appropriate for two reasons. First, the social-cognitive skills underlying empathy may be well developed by late adolescence/young adulthood. For example, Hoffman (2000) noted that the highest level of empathy is already achieved by late childhood or early adolescence. Other researchers have reported that perspective taking, role taking, internalization of norms/values and the internalization of affective reactions regarding the consequences of one's behavior on others increases from childhood to late adolescence (Davis & Franzoi, 1991; Eisenberg, Carlo, Murphy, & Van Court, 1995; Eisenberg, Cumberland, Guthrie, Murphy, & Shepard, 2005; Eisenberg & Fabes, 1998). Second, there are notable sex-related differences in empathy, with females showing greater empathizing. However, previous studies have noted that the range of empathy scores was slightly higher for males than for females (e.g., Baron-Cohen & Wheelright, 2004; Cowan & Khatchadourian, 2003; Knickmeyer, Baron-Cohen, Raggatt, Taylor, & Hackett, 2006). These sex differences may have been evolutionarily adaptive as female empathizing would have facilitated child rearing, stable relationships, and social hierarchies, whereas male empathizing would impede physical dominance (Baron-Cohen, 2005; Geary, 1998). Eisenberg and Fabes (1998) also noted that sex-related differences in empathy increased across childhood to adolescence possibly due to an increased emphasis on gender-related norms and expectations during this period. In the present study, we administered the Empathy Quotient (EQ; Baron-Cohen & Wheelright, 2004) because this self-report measure includes both cognitive and affective aspects of empathy (but these constructs are not separated in the scale). The EQ was also explicitly designed to have a clinical application and be sensitive to a lack of empathy as a feature of psychopathy (Lawrence, Shaw, Baker, Baron-Cohen & David, 2004). We hypothesized that individuals scoring low on the EQ would have smaller ERNs compared with those scoring higher on this measure. Although there is little research to date linking dopaminergic activity and empathy, Abu-Akel (2003) speculated that empathic abilities may be modulated, in part, by dopamine. Since the Pe has been found to be dissociable from the ERN in terms of both affective and dopaminergic influence, no relation was expected between empathy and the Pe. Similar to Dikman and Allen (2000) and Santesso et al. (2005) who reported no behavioral differences between high- and low-socialized individuals, we expect no relation between empathy and behavioral measures of performance monitoring.

Method

Participants

Thirty-nine males between the ages of 18 to 19 years ($M = 18.51$, $SD = .72$) recruited from Brock University participated. The majority of participants were Caucasian and right-handed. Each participant received $10 per hour for his participation.

Electrophysiological tasks

Participants completed the flanker task followed by the go/no-go task described in Chapter I, page 7.

Electrophysiological recording and data reduction

All recording and data reduction procedures were identical to those described in Chapter I, page 8.

Behavioral Measurements

The behavioral measurements used for this study were identical to those described in Chapter I, page 11.

Empathy Quotient (EQ). Empathy was measured using the Empathy Quotient (Baron-Cohen & Wheelright, 2004, see Appendix D) which includes 60 items (20 of which are filler-items). The EQ was designed to assess an individual's beliefs about his or her own empathic traits such as social sensitivity, sensitive communication. Participants are asked to indicate the degree to which they agree with a given statement on a 4-point scale. The EQ has been shown to be a reliable and valid method of measuring empathy in both healthy individuals and clinical populations (Lawrence, Shaw, Baker, Baron-Cohen, & David, 2004).

Results

Behavioral data

Flanker task. Table 4.1 presents the means (SD) for response time (RT), accuracy and post-error slowing across participants during the flanker and go/no-go task.[3] For the flanker task, a Category (Congruent, Incongruent) by Response (Correct, Error) ANOVA revealed a significant main effect for Category [$F(1, 38) = 16.2, p < .01$] and Response [$F(1, 38) = 53.3, p < .001$] indicating that RTs were faster for congruent compared with incongruent trials and for errors compared with correct responses. We also found that the percentage of errors on incongruent trials was higher than that on congruent trials [$F(1, 38) = 18.1, p < .001$]. A Category (congruent, incongruent) by Response (correct after correct RT, correct after error RT) ANOVA was performed to examine post-error slowing on incongruent trials. A significant main effect for Response indicated that participants showed post-error slowing across categories such that RTs were slower following errors than following correct responses [$F(1, 38) = 9.9, p = .003$].

To analyze response time for the go/no-go task, we performed an ANOVA with Category (go, no-go) as the within-subjects factor. There was no significant difference between the response time for correct go and incorrect no-go trials.

We also performed a series of Pearson correlations to examine the relations between the behavioral data on incongruent trials, incorrect no-go trials, and the personality measures but found no significant relations.

Error-related ERPs

Table 4.2 presents the means (SD) for the P3, ERN and Pe amplitudes for the flanker and go/no-go task. For the flanker task an ANOVA with Site (Fz, FCz, Cz, Pz) indicated that the P3 was maximal at Pz [$F(3, 114 = 7.6, p = .002$], the ERN was maximal at FCz [$F(3, 114) = 36.9, p < .001$], and the Pe was maximal at Pz [$F(3, 114) = 21.2, p < .001$]. Similar analyses were performed for the ERPs during the go/no-go task. The P3 was maximal at Pz [$F(3, 111) = 2.9, p = .07$], the ERN was maximal at FCz [$F(3, 111) = 26.8, p < .001$], and the Pe was maximal at Pz [$F(3, 108) = 21.1, p < .001$].

Empathy in relation to error-related ERPs

We performed a series of Pearson correlations to examine the relation between the error-related components (ERN, Pe) and empathy during the flanker (see Table 4.3). As can be seen in the scatter plots (Figure 4.1A and 4.1B), low scores on the empathy scale were associated with smaller to ERNs at FCz, $r = -.37, p = .02$ and at Cz, $r = -.36, p = .03$. The association between empathy and the Pe was not significant at any site. In a series of Pearson correlations, the P3 was unrelated to empathy ($p > .35$), but was related to the ERN during the flanker task (Fz $r = .72$; FCz $r = .48$; Cz $r = .49$, Pz $r = .62$; $p <= .001$). To ensure that variability related to the P3 preceding the ERN was not contributing to the present findings, we calculated ERN amplitude partialing out the variability due to the P3 using a regression method. ERN amplitude was the criterion variable while the P3 amplitude was entered as the independent variable and the residual ERN amplitude was saved. We found that the ERN findings were replicated at both FCz, $r = -.38$, $p = .02$, and Cz, $r = -.35$, $p = .03$, using this method.

To illustrate the association between empathy and the ERN for the flanker task, we made two groups based on a median split of the empathy scores: a high empathy ($M = 45.68$, $SD = 7.54$, n = 19) and a low empathy group ($M = 28.11$, $SD = 4.47$, n = 19) group. These two groups differed significantly in ERN amplitude at FCz, $t(37) = 2.2$, $p = .04$, and Cz, $t(37) = 2.4$, $p = .02$. Figure 4.2 displays the averaged response-locked ERP waveforms for high and low empathy groups for the flanker task. There were no significant group differences in mean RT, accuracy or post-error slowing.

There was a significant correlation between the ERN from the flanker and go/no-go task at FCz, $r = .51$, $p = .001$, and Cz, $r = .60$, $p < .001$. However, the Pe was not significantly related between tasks at Cz and Pz. Pearson correlational analyses were performed to examine the relation between empathy and the ERN and Pe during the go/no-go task. Again, the low empathy was associated with smaller ERNs at FCz, $r = -.37$, $p = .02$, and at Cz, $r = -.37$, $p = .02$ (see Figure 4.3A and 4.3B and Table 4.3). These relations also remained when we partialed out the P3 and analyzed the residualized ERN at FCz, $r = -.38$, $p = .02$, and Cz, $r = -.32$, $p = .05$.[5] There was no significant association between the Pe and empathy. Finally, there were no associations between the ERN or Pe and the behavioural measures for the flanker or go/no-go task.

We made another two groups based on a median split of the empathy scores during the go/no-go task: a high empathy ($M = 42.90$, $SD = 9.21$, $n = 21$) and a low empathy group ($M = 28.82$, $SD = 5.53$, $n = 17$) group[6]. These two groups differed significantly in ERN amplitude at FCz, $t(36) = 3.8$, $p = .001$, and Cz, $t(36) = 2.6$, $p = .01$. Figure 4.4 displays the averaged response-locked ERP waveforms for high and low empathy groups for the go/no-go task. There were no significant group differences in mean RT, accuracy or post-error slowing.

Discussion

We have provided the first electrophysiological study linking trait empathy to the ERN, an indirect index of ACC activity. Consistent with our hypotheses, low scores on the Empathy Quotient were associated with smaller ERNs during both a visual flanker and go/no-go task for 18- to 19-year-old males. Additionally, empathy scores did not relate to the Pe or behavioral performance measures.

The ERN results presented here are consistent with two previous reports linking the ERN to empathy-related constructs. First, Dikman and Allen (2000) reported that individuals scoring low (bottom 3% of all scores) on Gough's socialization scale had smaller ERNs than those scoring high (top 3% of all scores) on this measure. This scale is based on interpersonal behavior and perspective-taking theories of social deviance (i.e., the internalization of social experiences; Gough, 1994) and measures the willingness to accept norms/abide by rules and sensitivity towards the feelings and circumstances of others. Low-socialization scores have been consistently associated with impaired role-taking ability (Megargee, 1972; Rosen and Schalling, 1972), psychopathic personality (Edelmann & Vivian, 1988; Kosson, Smith, & Newman, 1990), passive-avoidance learning deficits (Nathan, 1980) and electrodermal hypo-responsiveness (Raine & Venables, 1984; Waid and Orne, 1982). Second, we previously reported that unselected 10-year-old children with poor social behaviors (i.e., high psychoticsm and low social desirability scores) displayed smaller ERNs (Santesso et al., 2005). These children could be characterized as apathetic/lacking empathy, indifferent to social expectations, under-socialized, with a tendency to engage in antisocial behaviors (Eysenck, 1991; Eysenck & Eysenck, 1976, 1994). This pattern of behaviour has also been consistently related to psychopathy in adults (Romero et al., 2001), insensitivity to rewarding experiences and weak inhibition in response to punishment signals (Revelle, 1995; Romero, et al., 2001). Dikman and Allen (2000) and Santesso and colleagues (Santesso et al., 2005) similarly concluded that low- or under-socialized individuals might have been less concerned about the consequences of having erred or, alternatively, did not monitor their performance as vigilantly as high-socialized individuals. A lack of empathy (measured here) may also be associated with inappropriate affective reactions, antisocial and psychopathic tendencies (e.g., Baron-Cohen, 2004). Taken together, these results suggest that these individuals may be unable to experience or appreciate the emotional significance of errors or other unfavorable outcomes.

In another recent study, Bates and colleagues (Bates, Patel, & Liddle, 2005) observed an ERN in adults who either performed, or observed others performing and committing errors on a go/no-go task. The observer was able to see the same computer display and key-press and therefore had access to visual cues signalling that an error response would, and did occur. The authors speculated that the ERN might reflect 'mirroring' of error detection and provide insight into how individuals monitor others, which may be particularly important for understanding disorders characterized by empathic deficits: psychopathology, schizophrenia and autism. Trait empathy and/or empathy-related personality measures were not assessed in the study conducted by Bates and colleagues, so it would be interesting to examine empathy and the observation of errors (as well as other empathy-inducing scenarios) in the same study. We speculate that low empathy would be related to poor error monitoring (as indexed by smaller ERNs) in both the performed and observed conditions.

Our finding that individuals scoring low on empathy had smaller ERNs (or high empathy and larger ERNs) is also consistent with neuroimaging studies linking empathy to activity of the ACC. ACC hypoactivity has been observed in relation to apathy in demented and non-demented elderly patients (Migneco et al., 2001) and in psychopathic individuals while processing (i.e., during encoding and recognition of) negative affective words (Kiehl et al., 2001). Finally, Singer and colleagues (2004) demonstrated increased activation in the rostral ACC while adults either experienced a painful stimulus or when they observed a signal indicating that their loved one experienced pain (this latter condition induced empathy). ACC activation also correlated with self-reported empathy scores. It appears that the ERN is not only a useful indirect measure of ACC activity, but perhaps empathic abilities.

Although no studies have directly examined dopamine in relation to empathy and the ERN, Abu-Akel (2003) hypothesized that theory of mind, a fundamental process in empathizing, may be linked to dopaminergic-serotonergic (DS) systems. He noted that DS systems innervate regions in the PFC that mediate theory of mind, with serotonin modulating dopaminergic activity (Milan, 2000). Dysregulation of this system may be linked to impairments in theory of mind (i.e., making guesses or predictions about the intentions, affect and knowledge of others), as is the case with schizophrenia and autism (Croonenberghs et al., 2000; Herault et al., 1993; Keefe & Harvey, 1994; Meltzer & McGurk, 1999). Disruption of the dopamine system (either directly or by modulation of the serotonergic system) "could lead to the generation of erroneous predictions about the content of the mind of others…or the inability to generate predictions" (p. 384). Theory of mind errors and the formation of rewarding social interactions is, in his view, no different than the reinforcement learning system outlined by Schultz and colleagues (Schultz, et al., 1997). Our finding that low empathy was associated with smaller ERNs (which may be indicative of dopaminergic dysfunction) fits this hypothesis. Future studies should, however, examine more directly the association between dopaminergic activity, empathy, and the ERN.

Consistent with previous studies reporting no relation between the Pe and affective style, we found that the Pe was unrelated to empathy. These findings largely underscore the dissociable properties of the Pe and ERN. This dissociation may be due to differences in the neural generators and/or differential influence of dopaminergic activity (e.g., Falkenstein et al., 2005).

Several limitations of the present study must be noted. First, we examined males because males tend to score lower on measures of empathy and display more antisocial tendencies than women and may therefore have a greater range of scores on the empathy measure. Of course, the range of scores would increase even more if women were included. Similar issues should be examined in women before generalizations can be made (it is unclear, however, what the sex distribution in Dikman and Allen's study was). Second, unlike Dikman and Allen (but similar to Santesso et al. 2005) our sample was unselected and, therefore, the empathy scores obtained were not extreme values. The range of scores in our sample was 15-62 with high- and low-empathy group means around 46 and 28, respectively. The EQ was designed to have a clinical application and be sensitive to a lack of empathy as a feature of psychopathology (Lawrence et al., 2004). The average score on this scale ranges from 33-52 (most men score about 42), above average/very high scores range from 53-63/64-80, and low scores range from 0-32 (those with Asperger's Syndrome score about 20) (Baron-Cohen & Wheelright, 2004). No males in our study scored in the very high empathy range and only five males scored around 20 (+/-5 points). Our findings might have been attenuated by this distribution of scores but it is still important to note that the findings can be extended to late adolescence/young adulthood within a normal range of empathic ability. Third, although the EQ measures both cognitive and affective empathy, it is impossible to disentangle the two aspects or to examine related constructs such as perspective-taking and shared representations which may be associated with activity of different PFC regions. Fourth, this study used a self-report measure of empathy, while some other studies have tested participants actively empathizing (e.g., making empathic judgements, observing another). In the first instance, the person is making a decision about their own *trait* but in the second instance, participants are actively engaged in the *state*. Although the studies reviewed here point to a significant role of the PFC in both trait and state empathy, activity in specific PFC regions may differ. Future studies should examine error-related ERPs while participants are empathizing (e.g., an observational scenario, Bates et al., 2005) and while performing standard learning paradigms.

In summary, the present study supports the hypothesis that the ERN is sensitive to motivation/goal states and the degree to which individuals are concerned about the outcome of an event. The Pe, however, is less affected by affective style (i.e., empathy) and is dissociable from the ERN. Low empathic individuals (within the normal range) may therefore display poor error monitoring and affective reactions to errors as opposed to error recognition. It is possible that the relation between empathy and the ERN reported here was mediated by the dopamine system as the cognitive processes involved in empathizing rely heavily on areas rich in dopamine and disruptions in the dopamine system can lead to impaired theory of mind/empathizing. The results of the present study have important implications for understanding how diminished responsiveness to unfavorable outcomes may be associated with psychopathic tendencies. The results also suggest that the ERN may be useful index of ACC activity and an important marker of empathic and perspective taking deficits in late adolescents/young adults and possibly throughout the development of moral behavior and the internalization of societal values/norms in childhood.

General Discussion

Traditional psychologists argued that the human brain was fully developed by early childhood. Today, however, we know that there are important changes occurring in the structure and function of brain as well as in brain neurotransmitter systems throughout childhood and adolescence. Despite significant gains in the fields of neuroscience, surprisingly little is known about the developing human brain, particularly throughout adolescence. Over the last four decades, researchers have noted delayed maturation of the prefrontal cortex and surrounding cortices by measures of myelination (Yakovlev & Lecours, 1967; Pfefferbaum et al., 1993), gray matter reduction (Jernigan et al., 1991; Pfefferbaum et al., 1993; Sowell et al., 2001), synaptogenesis (Huttenlocher, 1979), resting metabolism (Chugani et al., 1987; Casey et al., 2000) and dopaminergic innervation (Benes et al., 1996; Kalsbeek et al., 1988; Lambe et al., 2000). These dynamic brain changes are influenced by environmental information such as stress and early perceptual and social experience (see Cynader & Frost, 1999 for review).

Personality also continues to develop into adulthood (see Srivastava, John, Gosling, & Potter, 2003). Erikson (1959), for example, argued that personality developed far beyond puberty and through old age. Research suggests that personality, or affective style, may have robust effects on various cognitive processes such as the way individuals encode, interpret, recall, and act upon the external world (McNally, 1998). Additionally, the activation of discrete brain regions and/or patterns of cortical activation may be associated with affective responses to events (such as performance errors). How vigilantly one monitors, learns from, and emotionally responds to their performance may be particularly useful in understanding maladaptive social behaviors, and one's propensity to engage in and evaluate risky events throughout development.

Fortunately, ERPs offer a non-invasive and relatively inexpensive method for assessing the functional maturation of the brain and the integrity of the performance monitoring system. The collection of studies presented here has demonstrated that error-related ERPs (particularly the ERN) are reliable across time, thus providing a useful index of performance monitoring. Moreover, the findings are consistent with imaging studies locating the generator of the ERN to the ACC and delayed maturation of this region. Longitudinal testing, however, may better assess brain and personality changes that occur with development. More studies are also needed to determine whether or not the ERN can be used as a reliable index of dopaminergic activity via a reinforcement learning signal.

Footnotes

[1]This procedure displays the residual scalp ERP with the bipolar eye channel signal removed on a trial-to-trial basis, permitting manual rejection of the trial in the rare case when there is overcorrection. This method thus reduces noise introduced by overcorrection that is occasionally found in automated eye correction procedures.

[2]We examined error-related ERPs in males only for two reasons. First, this developmental study was part of a larger study examining hormonal and personality differences in male adolescents and young adults. Second, in their developmental study, Davies and colleagues (2004) noted a reduction in ERN amplitude at ages 10 and 13 years and subsequent fluctuations through adolescence, suggestive of pubertal effects. For girls, the ERN amplitude was lowest at age 10 and increased linearly with age. For boys, the ERN amplitude was lowest at age 13 and both linear and quadratic effects were apparent (peaking at around 18 years of age). In order to avoid possible sex-related differences (both dopaminergic and hormonal) we limited our sample to males.

[3]The go/no-go task increased in speed with correct responding and decreased in speed with incorrect responding; thus, this task was not conducive to examining post-error slowing.

[4] We also performed a multiple regression and added Positive outcome expectancies as a predictor in the analysis. None of the variables contributed for a significant amount of unique variability in the ERN, and the model accounted for 31.4% of the total variance.

[5]We also measured the peak-to-peak ERN as the amplitude of the most positive peak before the onset of the ERN (i.e., the P3) minus the most negative peak (i.e., the ERN) in the time window of 20-150 ms after an incorrect key press. Pearson correlations between the peak-to-peak ERNs during the flanker and go/no-go tasks were unrelated to empathy. This measure, however, includes separate, additive variance from both the P3 peak and ERN deflection and

may have attenuated the relation. The use of the residualized ERN controls for variability in the ERN due to the P3 and therefore provides a better measure.

[6]For each of the tasks, a different participant did not have scorable ERPs. Therefore the median split used to determine high- and low-empathy groups differ between tasks as well as the number of participants in each group.

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Table 1.1

Means (SD) of response times, response time variability, percentage of errors and post-error slowing for the flanker task at time 1 and 2

	Congruent		Incongruent	
	Correct	Error	Correct	Error
		Time 1		
Response time	412.30 (87.79)	303.22 (98.64)	432.30 (97.65)	364.69 (109.83)
Response time variability	117.3 (37.27)	81.23 (40.34)	129.54 (56.67)	106.83 (45.51)
Percentage of errors		.18 (.23)		.24 (.19)
Post-error slowing		29.47 (64.52)		11.70 (47.53)
		Time 2		
Response time	439.48 (77.51)	346.06 (94.37)	468.28 (94.13)	388.24 (99.41)
Response time variability	121.59 -10.33 (31.18)	98.27 (39.10)	128.37 -18.79 (32.31)	126.01 (43.42)
Percentage of errors		.12 (.08)		.17 (.09)
Post-error slowing		10.33 (51.39)		18.79 (54.16)

Table 1.2

Means (SD) of response times, response time variability and percentage of errors for the go/no-go task at time 1 and 2

Response measure	Correct Go	Error No-go
	Time 1	
Response time	331.24 (57.93)	321.98 (72.09)
Response time variability	134.41 (21.49)	128.14 (43.36)
Percentage of errors		.35 (.10)
	Time 2	
Response time	344.37 (60.77)	342.95 (69.08)
Response time variability	143.86 (28.52)	144.65 (40.16)
Percentage of errors		.33 (.11)

Table 1.3

Pearson correlations for accuracy, response time (RT) and post-error slowing for the flanker and go/no-go tasks at time 1 and 2

	Pearson correlation
Flanker	
Percentage of congruent errors	.12
Percentage of incongruent errors	.21
RT congruent errors	.36
RT congruent correct	.49*
RT incongruent errors	.33
RT incongruent correct	.48*
Post-error slowing, congruent trials	.27
Post-error slowing, incongruent trials	.34
Go/no-go	
Percentage of no-go errors	.62**
RT no-go errors	.53*
RT correct go	.74**

*p < .05, two-tailed. **p < .01, two-tailed

Table 1.4

Means (SD) of the ERN and Pe at each site during the flanker task at time 1 and 2

	Time 1			
	Fz	FCz	Cz	Pz
P3	1.93 (3.34)	3.32 (3.38)	4.56 (3.85)	4.73 (3.72)
ERN (base-to-peak)	-3.50 (4.02)	-4.92 (4.35)	-3.44 (4.12)	.63 (3.93)
ERN (peak-to-peak)	5.34 (3.03)	8.25 (4.20)	8.19 (3.90)	4.46 (2.73)
ERN (residualized)	.29 (.81)	.35 (..79)	.40 (.79)	.36 (.91)
Pe	1.46 (3.63)	4.40 (5.36)	6.17 (4.82)	7.04 (4.18)
	Time 2			
	Fz	FCz	Cz	Pz
P3	1.44 (3.78)	2.91 (3.61)	4.60 (3.75)	4.58 (3.77)
ERN (base-to-peak)	-2.22 (3.44)	-2.95 (3.83)	-1.57 (3.19)	.64 (2.41)
ERN (peak-to-peak)	4.02 (2.01)	6.25 (2.48)	6.62 (3.29)	4.35 (3.06)
ERN (residualized)	.29 (.72)	.39 (.64)	.44 (.64)	.18 (.90)
Pe	1.87 (3.64)	3.05 (2.81)	5.56 (2.23)	6.14 (2.90)

Table 1.5

Means (SD) for the P3, ERN and Pe at each site during the go/no-go task at time 1 and 2

	Time 1			
	Fz	FCz	Cz	Pz
P3	.77 (3.89)	.85 (3.89)	1.56 (3.64)	3.65 (3.05)
ERN (base-to-peak)	-3.02 (3.29)	-4.44 (3.85)	-3.13 (3.67)	.40 (2.99)
ERN (peak-to-peak)	3.72 (2.20)	5.01 (2.80)	4.44 (2.79)	2.99 (1.97)
ERN (residualized)	.28 (.73)	.30 (.80)	.29 (.82)	.41 (.73)
Pe	.87 (2.32)	2.92 (3.21)	5.53 (4.20)	6.51 (1.07)

	Time 2			
	Fz	FCz	Cz	Pz
P3	1.49 (2.96)	1.46 (2.66)	1.63 (2.84)	2.75 (2.76)
ERN (base-to-peak)	-3.28 (3.00)	-4.34 (3.02)	-3.66 (3.07)	-.75 (2.85)
ERN (peak-to-peak)	4.87 (1.84)	5.81 (2.32)	5.31 (2.53)	3.70 (2.15)
ERN (residualized)	.05 (.98)	.08 (1.05)	.12 (1.03)	.19 (.83)
Pe	.42 (2.03)	1.95 (1.92)	4.21 (2.47)	4.90 (2.85)

Table 1.6

Pearson (r) and intraclass (r') correlations for the P3, ERN and Pe for the flanker task

Site		r	r'
Fz	P3	.06	.08
	ERN (base-to-peak)	.11	.09
	ERN (peak-to-peak)	.33	.30
	ERN (residualized)	.30	.31
	Pe	.36	.38*
FCz	P3	.16	.17
	ERN (base-to-peak)	.24	.18
	ERN (peak-to-peak)	.65**	.54**
	ERN (residualized)	.55**	.56**
	Pe	.53**	.42*
Cz	P3	.31	.33*
	ERN (base-to-peak)	.13	.07
	ERN (peak-to-peak)	.53**	.50**
	ERN (residualized)	.41*	.42*
	Pe	.53**	.41*
Pz	P3	.37	.39*
	ERN (base-to-peak)	-.03	.00
	ERN (peak-to-peak)	.58**	.59**
	ERN (residualized)	.31	.31*
	Pe	.33	.30*

Table 1.7

Pearson (*r*) and intraclass (*r*') correlations for the P3, ERN and Pe for the go/no-go task

Site		*r*	*r'*
Fz	P3	.25	.26
	ERN (base-to-peak)	.31	.32
	ERN (peak-to-peak)	.36	.21
	ERN (residualized)	.35	.23
	Pe	.19	.19
FCz	P3	.36	.36*
	ERN (base-to-peak)	.60**	.60**
	ERN (peak-to-peak)	.41	.42*
	ERN (residualized)	.52**	.47*
	Pe	.29	.23
Cz	P3	.25	.27
	ERN (base-to-peak)	.59**	.56**
	ERN (peak-to-peak)	.39	.41*
	ERN (residualized)	.54**	.54**
	Pe	.66**	.54**
Pz	P3	.38	.31
	ERN (base-to-peak)	.32	.25
	ERN (peak-to-peak)	.05	.07
	ERN (residualized)	.18	.19
	Pe	.63**	.52**

Table 2.1

Means (SD) of response time, response time variability, percentage of errors and post-error slowing during the flanker task for 15- and 18-year-olds

	Congruent		Incongruent	
Response measure	Correct	Error	Correct	Error
		15-year-olds		
Response time	408.09 (96.73)	305.56 (98.13)	424.52 (96.96)	352.87 (105.41)
Response time variability	119.65 (39.37)	86.73 (39.76)	132.62 (57.59)	108.67 (47.90)
Post-error slowing		35.55 (61.67)		14.50 (46.45)
Percentage of errors		.17 (.22)		.24 (.18)
		18-year-olds		
Response time	443.01 (66.63)	314.15 (141.04)	469.70 (71.09)	357.62 (104.52)
Response time variability	118.24 (29.78)	87.65 (53.09)	120.57 (33.27)	86.43 (46.52)
Post-error slowing		33.43 (76.56)		30.24 (76.60)
Percentage of errors		.12 (.20)		.16 (.20)

Table 2.2

Means (SD) of response time, response time variability and percentage of errors during the go/no-go task for 15- and 18-year-olds

Response measure	Correct Go	Error No-go
	15-year-olds	
Response time	335.83 (57.11)	326.16 (72.02)
Response time variability	137.53 (24.25)	127.06 (39.28)
Percentage of errors		.34 (.10)
	18-year-olds	
Response time	340.37 (61.72)	340.67 (80.43)
Response time variability	124.79 (25.80)	120.24 (40.34)
Percentage of errors		.29 (.09)

Table 2.3

Means (SD) of error-related ERPs during the flanker task for 15- and 18-year-olds

	Site			
	Fz	FCz	Cz	Pz
		15-year-olds		
ERN	-3.51 (4.12)	-5.11 (3.73)	-4.20 (3.92)	-.29 (3.67)
P3-ERN	5.36 (2.71)	8.14 (3.34)	8.61 (3.83)	4.71 (2.48)
Pe	2.22 (5.41)	4.38 (5.71)	6.71 (5.09)	7.99 (5.02)
P3-CRN	2.41 (2.05)	3.15 (1.93)	3.38 (2.08)	2.92 (2.16)
		18-year-olds		
ERN	-4.52 (4.87)	-7.33 (3.84)	-6.13 (3.95)	-1.43 (3.55)
P3-ERN	6.56 (2.57)	9.81 (3.53)	9.65 (3.88)	6.26 (3.19)
Pe	2.32 (7.07)	3.92 (5.87)	5.68 (5.50)	6.80 (4.94)
P3-CRN	2.06 (1.67)	2.83 (2.06)	2.63 (1.84)	2.62 (1.89)

Table 2.4

Means (SD) of error-related ERPs during the go/no-go task for 15- and 18-year-olds

	Site			
	Fz	FCz	Cz	Pz
	15-year-olds			
ERN	-3.25 (2.97)	-4.81 (3.46)	-3.63 (3.38)	-.22 (3.12)
P3-ERN	4.39 (2.34)	6.03 (3.17)	5.41 (3.15)	3.89 (2.37)
Pe	1.55 (2.41)	3.92 (3.73)	6.35 (4.09)	7.06 (3.49)
P3-CRN	1.74 (1.37)	1.58 (1.56)	1.32 (1.36)	—
	18-year-olds			
ERN	-4.24 (3.35)	-7.00 (3.79)	-6.26 (3.87)	-2.37 (3.88)
P3-ERN	6.22 (2.57)	8.54 (3.53)	7.86 (3.88)	5.63 (3.19)
Pe	2.96 (4.75)	5.02 (4.85)	6.86 (4.54)	7.17 (4.17)
P3-CRN	2.27 (1.85)	1.94 (1.93)	1.20 (1.36)	—

Table 3.1

Means (SD) of response time, percentage of errors and post-error slowing during the flanker task

	Congruent		Incongruent	
	Correct	Error	Correct	Error
Response time	438.74 (70.09)	295.09 (121.33)	463.6 (72.18)	334.05 (99.85)
Percentage of errors		12.04 (.22)		16.82 (.21)
Post-error slowing		40.91 (82.37)		32.88 (77.52)

Table 3.2

Means (SD) of error-related ERPs at each site during the flanker task

	Site			
	Fz	FCz	Cz	Pz
ERN	-5.23 (5.16)	-8.17 (4.75)	-7.21 (5.17)	-2.27 (4.27)
P3-ERN	7.75 (3.68)	11.63 (5.18)	11.61 (5.45)	7.57 (4.02)
Pe	2.82 (7.30)	4.59 (6.38)	6.33 (6.17)	7.59 (5.73)
P3-CRN	2.5 (1.79)	3.1 (2.02)	2.76 (1.74)	2.79 (1.68)

Table 3.3

Correlations among the personality measures ERN amplitude at Cz

Variable	1	2	3	4	5	6	7
1. Risk-taking	—	.54**	.37*	-.08	.38*	-.01	.43**
2. Sensation seeking			.42**	-.05	.21	-.05	.44**
3. Sensitivity to reward				.06	.12	.03	.38**
4. Sensitivity to punishment					.17	.01	.25
5. Positive outcome expectancies						-.47	.33
6. Negative outcome expectancies							-.10
7. ERN amplitude at Cz							—

Note. *p < .05, **p < .01 (two-tailed). Greater negativity on the ERN indicates greater amplitude.

Table 3.4

Results from the multiple regression analysis predicting ERN amplitude at Cz from Risk-taking, Sensation Seeking and Sensitivity to Reward (N = 38)

Variable	B	SE B	β	sr^2
Risk-taking	.11	.08	.24	.04
Sensation seeking	.22	.18	.22	.03
Sensitivity to reward	.26	.21	.20	.03

Note. $R^2 = .28$ ($p = .01$).

B = Beta; SEB = standard error of Beta; sr^2 = squared semi-partial correlation

Table 4.1

Means (SD) of response time, percentage of errors and post-error slowing during the flanker task and go/no-go task

Flanker task	Congruent		Incongruent	
	Correct	Error	Correct	Error
Response time	442.84 (70.86)	307.54 (139.69)	469.32 (73.31)	357.89 (107.18)
Percentage of errors		12.00 (20.95)		16.40 (20.19)
Post-error slowing		34.34 (74.91)		34.72 (75.88)

Go/no-go task	Go	No-go
Response time	338.33 (60.89)	335.03 (80.60)
Percentage errors		28.96 (9.67)

Table 4.2

Means (SD) of error-related ERPs during the flanker and go/no-go task

	Fz	FCz	Cz	Pz
Flanker task				
P3	2.25 (4.88)	2.92 (5.24)	3.64 (5.28)	4.57 (4.56)
ERN	-5.23 (4.52)	-8.68 (4.37)	-8.19 (5.12)	-3.26 (4.35)
Pe	2.17 (6.89)	4.39 (6.45)	6.22 (6.16)	7.45 (5.38)
Go/no-go task				
P3	2.69 (3.78)	2.29 (4.31)	2.26 (4.31)	3.62 (3.92)
ERN	-4.48 (3.26)	-7.39 (3.79)	-6.68 (3.76)	-2.86 (4.19)
Pe	3.19 (4.81)	5.37 (5.03)	7.29 (4.50)	7.28 (4.19)

Table 4.3

Correlations between the ERN and empathy during the flanker and go/no-go task

	Empathy
Flanker task	
FCz ERN (base-to-peak)	-.37*
Cz ERN (base-to-peak)	-.36*
FCz ERN (residualized)	-.38*
Cz ERN (residualized)	-.35*
Go/no-go task	
FCz ERN (base-to-peak)	-.37*
Cz ERN (base-to-peak)	-.37*
FCz ERN (residualized)	-.38*
Cz ERN (residualized)	-.32*

Note. $*p < .05$, $**p < .01$ (two-tailed). Greater negativity on the ERN indicates greater amplitude.

Figure 1.1

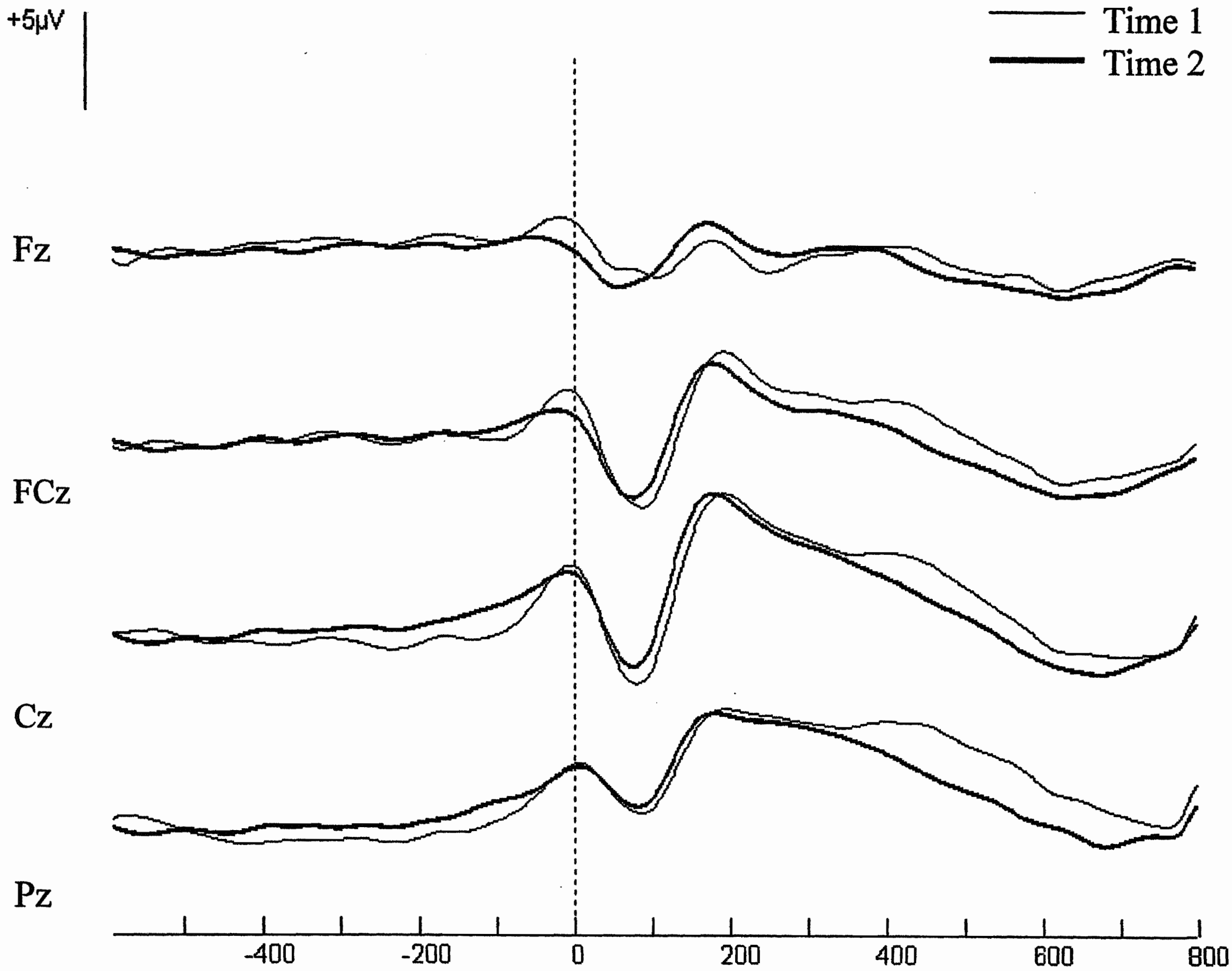


Figure 1.2

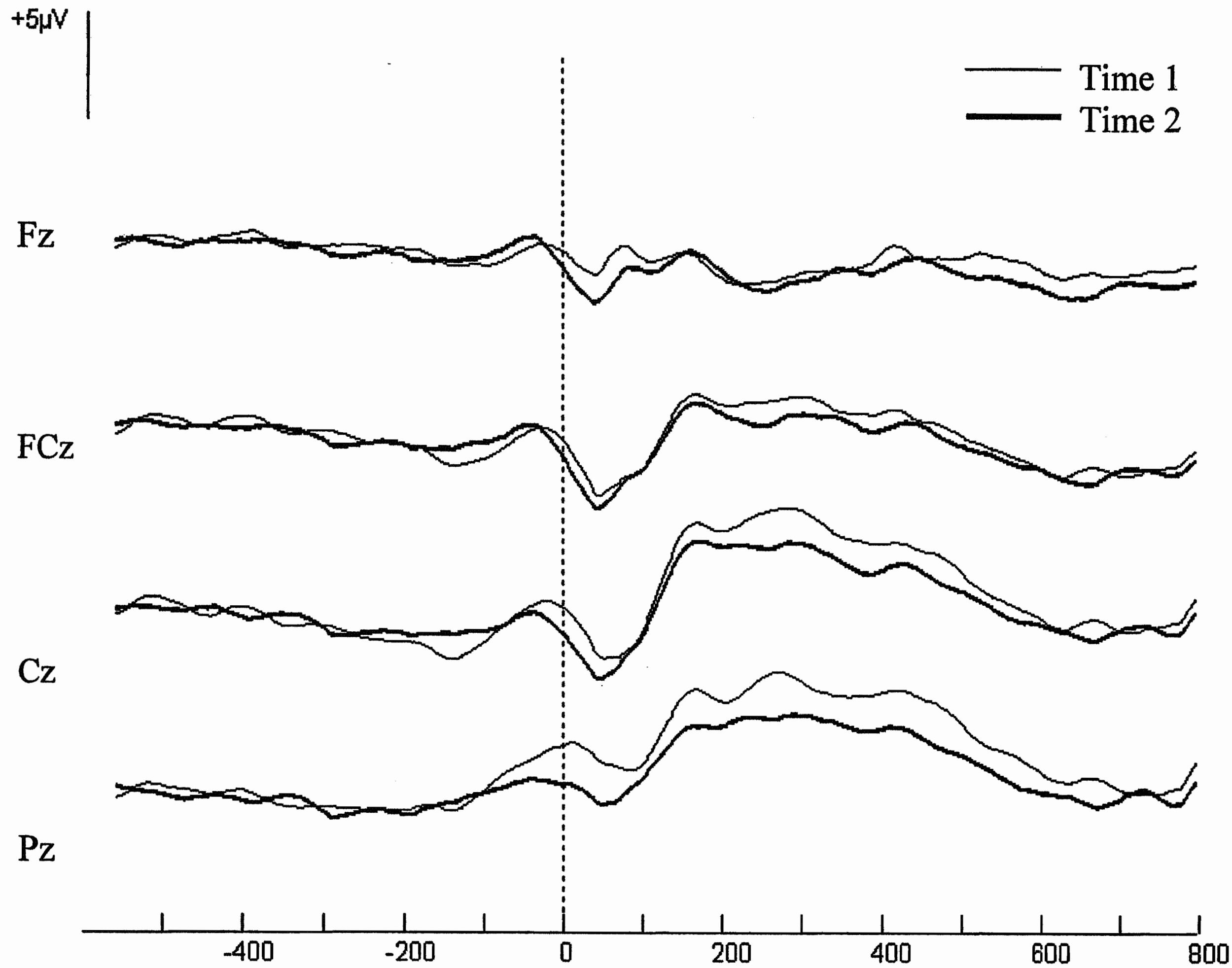


Figure 2.1

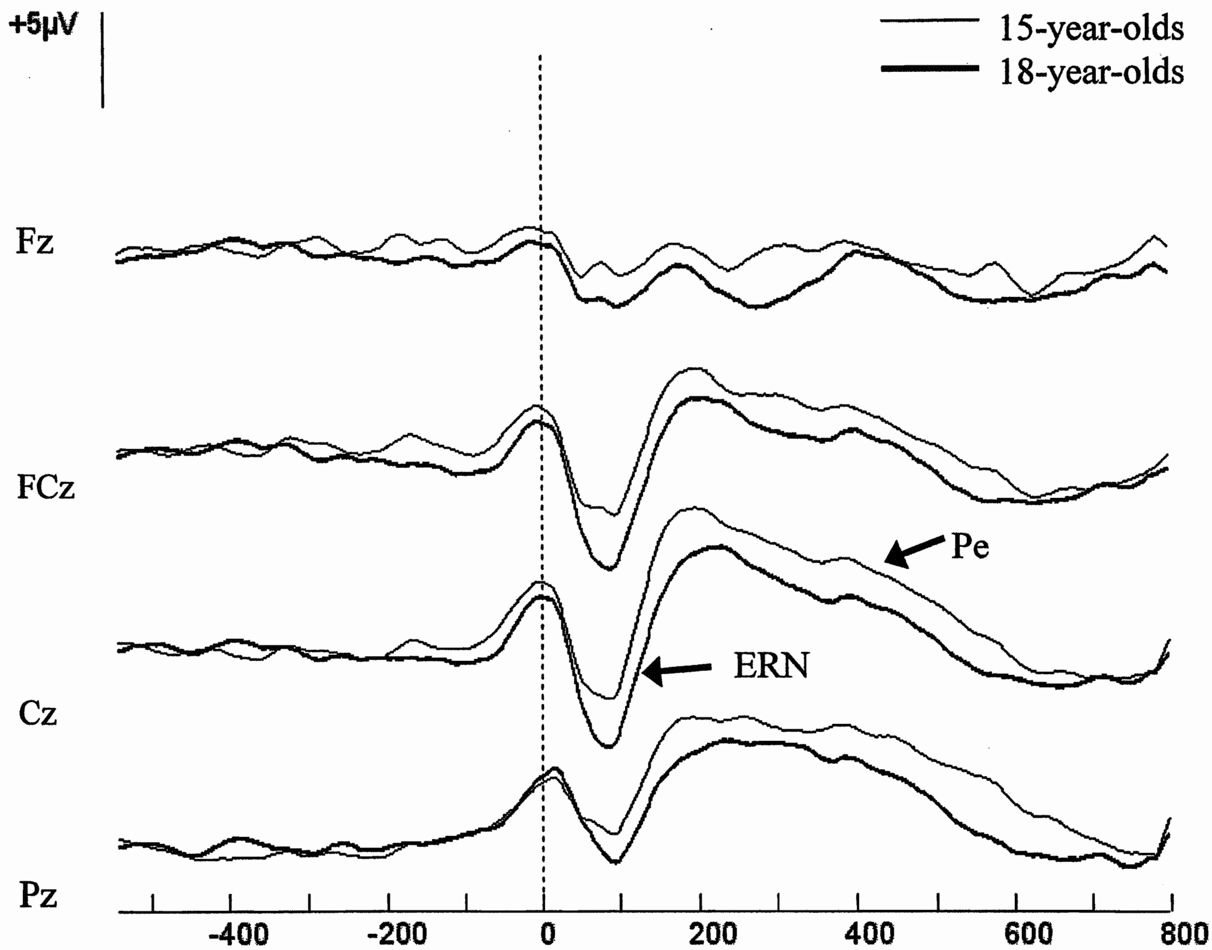

+5μV
15-year-olds
18-year-olds
Fz
FCz
Cz
Pz
Pe
ERN
-400
-200
0
200
400
600
800

Figure 2.2

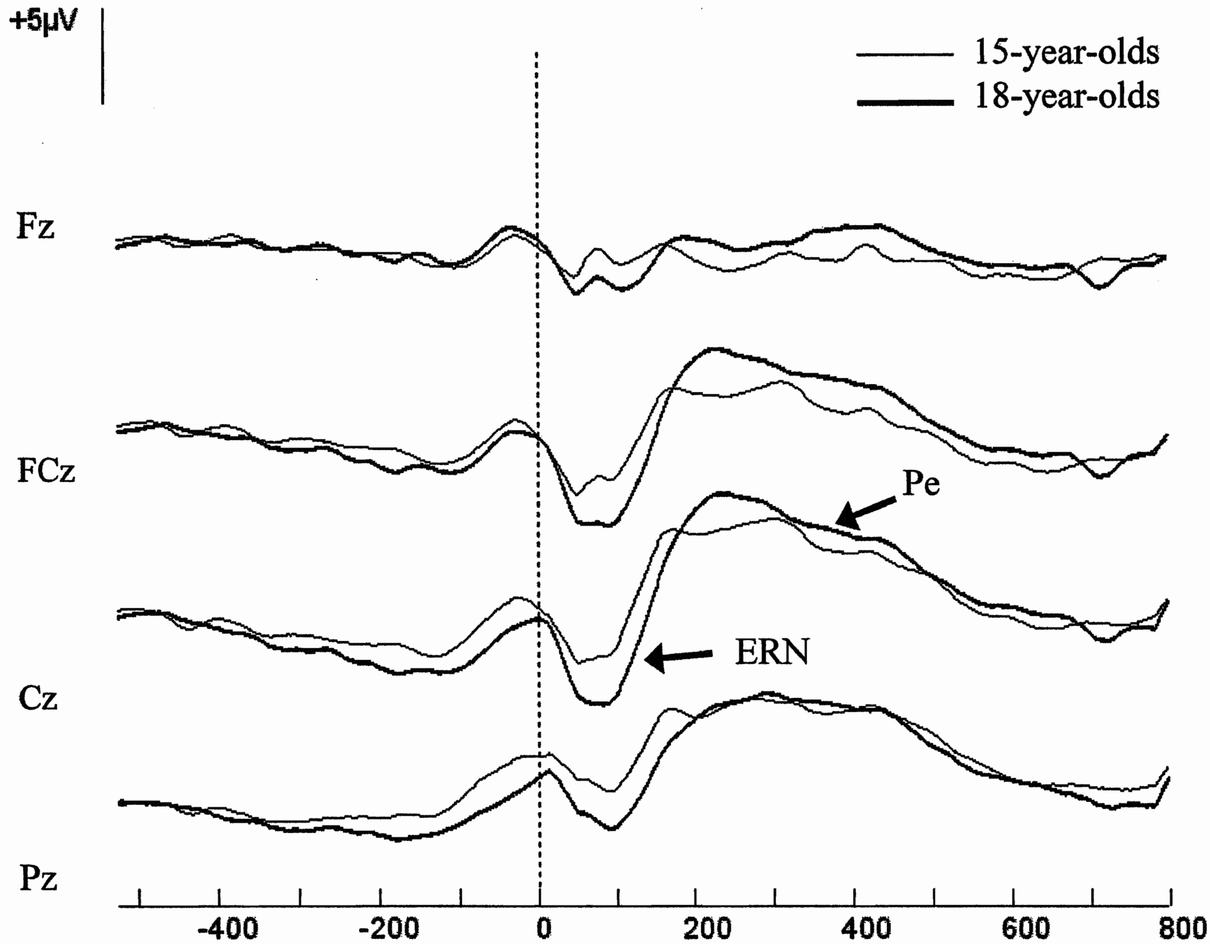
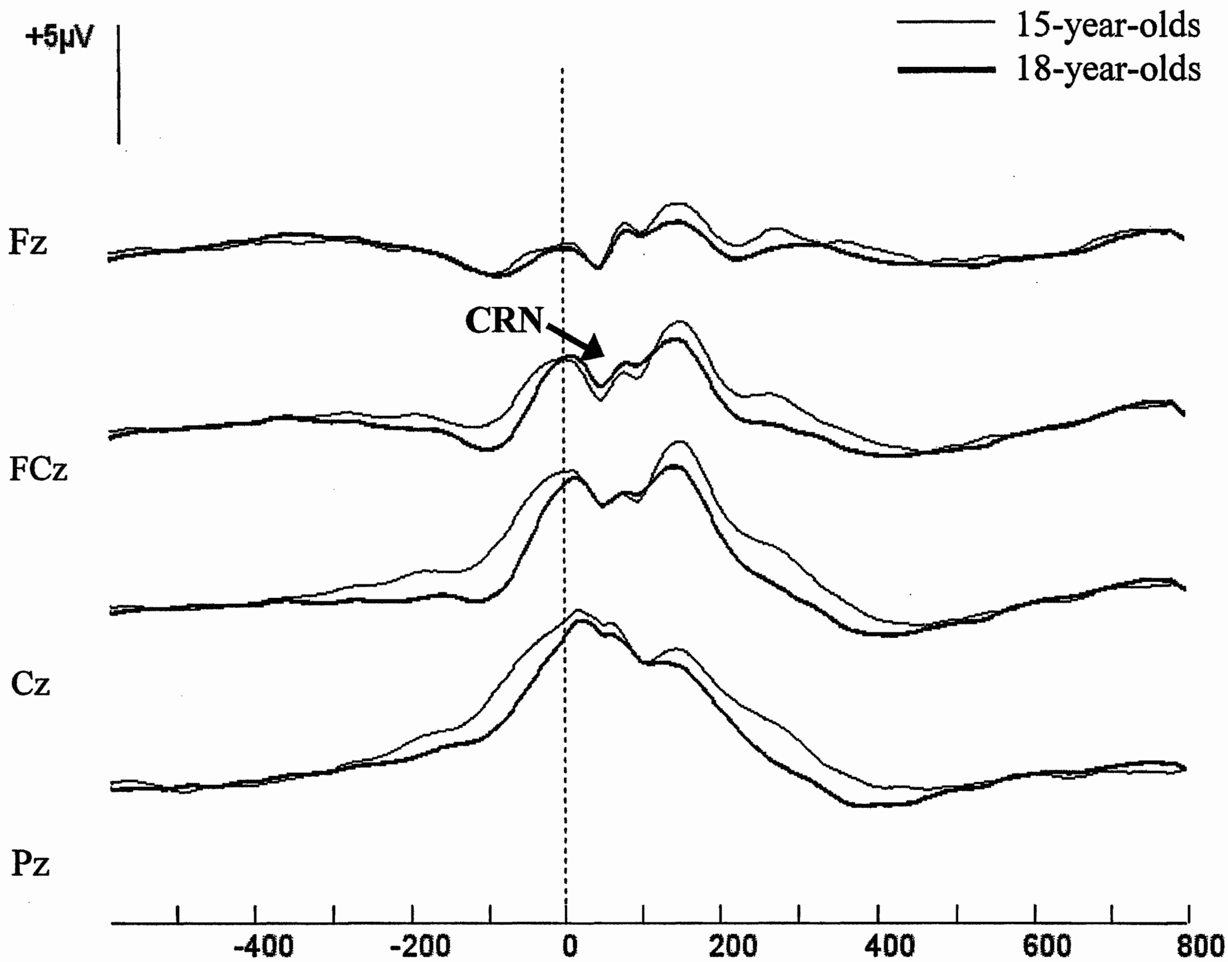

+5μV
15-year-olds
18-year-olds
Fz
FCz
Cz
Pz
Pe
ERN
-400
-200
0
200
400
600
800

Figure 2.3



+5µV
15-year-olds
18-year-olds
Fz
CRN
FCz
Cz
Pz
-400
-200
0
200
400
600
800

Figure 2.4

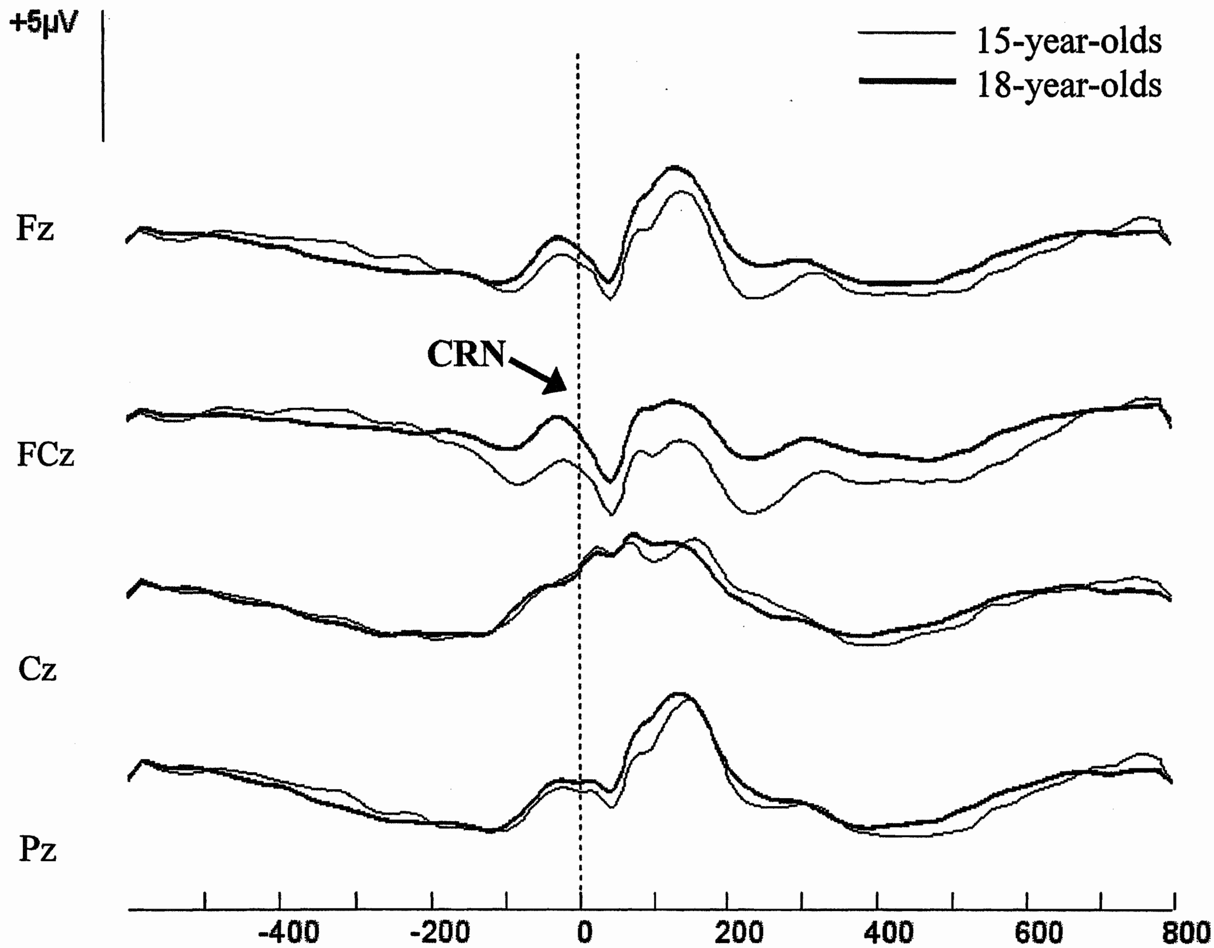

+5µV
15-year-olds
18-year-olds
Fz
CRN
FCz
Cz
Pz
-400
-200
0
200
400
600
800

Figure 3.1A

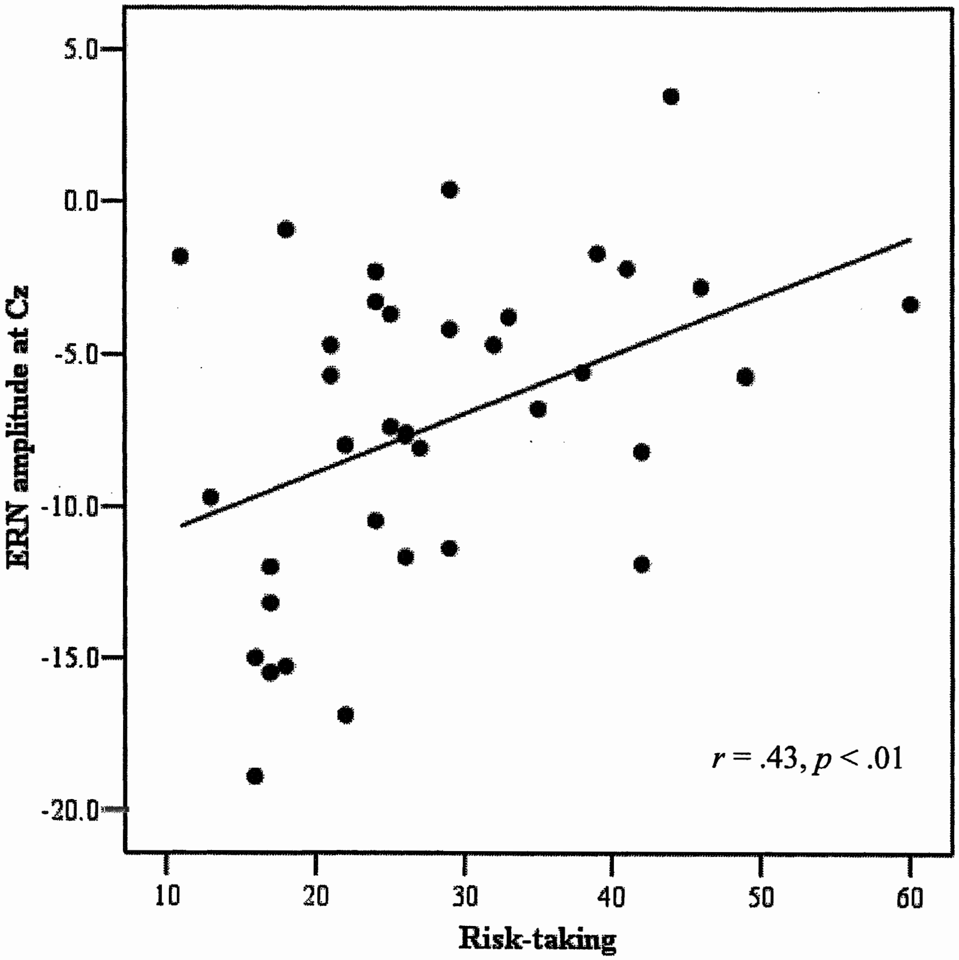

5.0
0.0
-5.0
-10.0
-15.0
-20.0
ERN amplitude at Cz
10
20
30
40
50
60
Risk-taking
r = .43, p < .01

Figure 3.1B

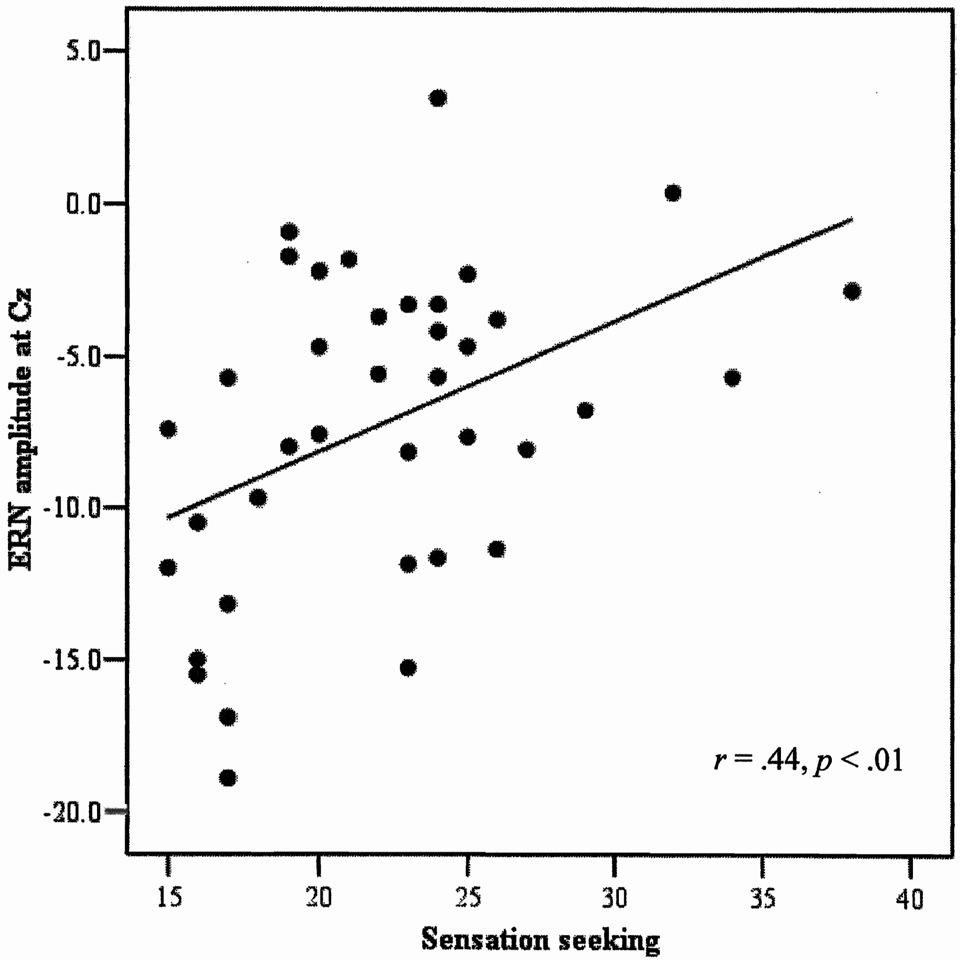

5.0
0.0
-5.0
-10.0
-15.0
-20.0
ERN amplitude at Cz
15
20
25
30
35
40
Sensation seeking
$r = .44, p < .01$

Figure 3.1C

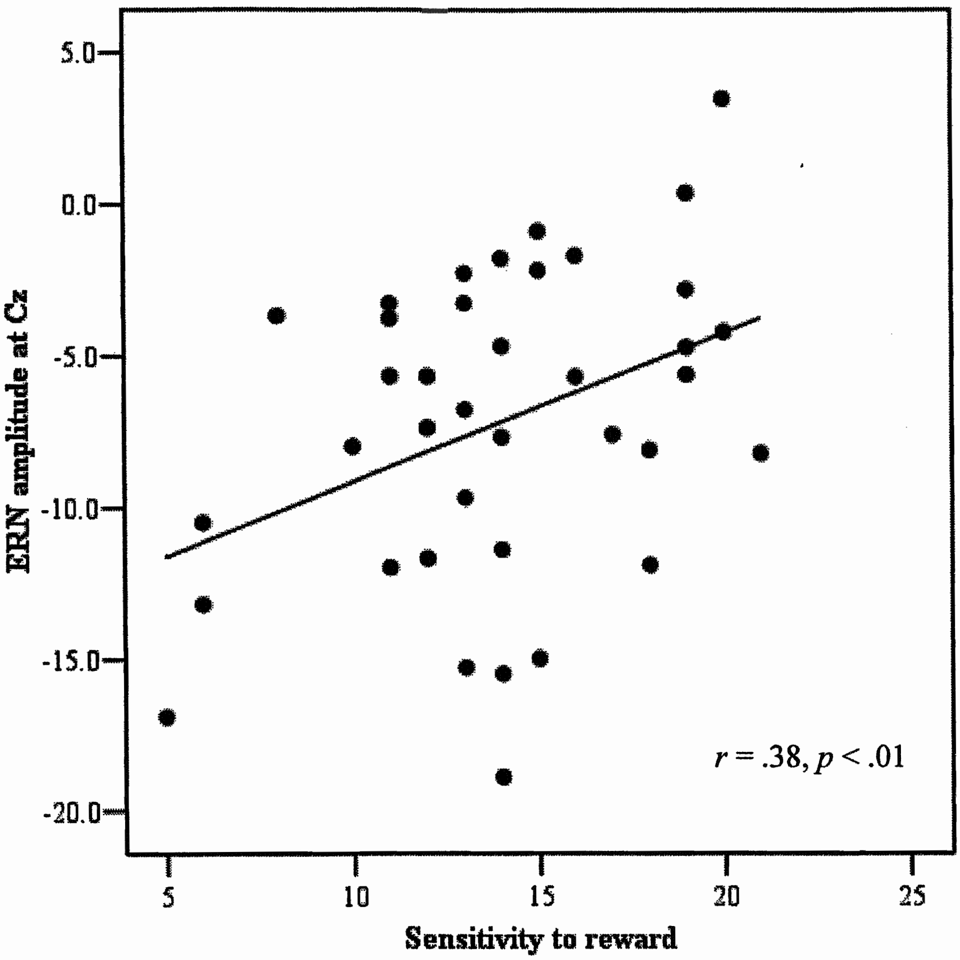

5.0
0.0
-5.0
-10.0
-15.0
-20.0
ERN amplitude at Cz
5
10
15
20
25
Sensitivity to reward
r = .38, p < .01

Figure 3.1D

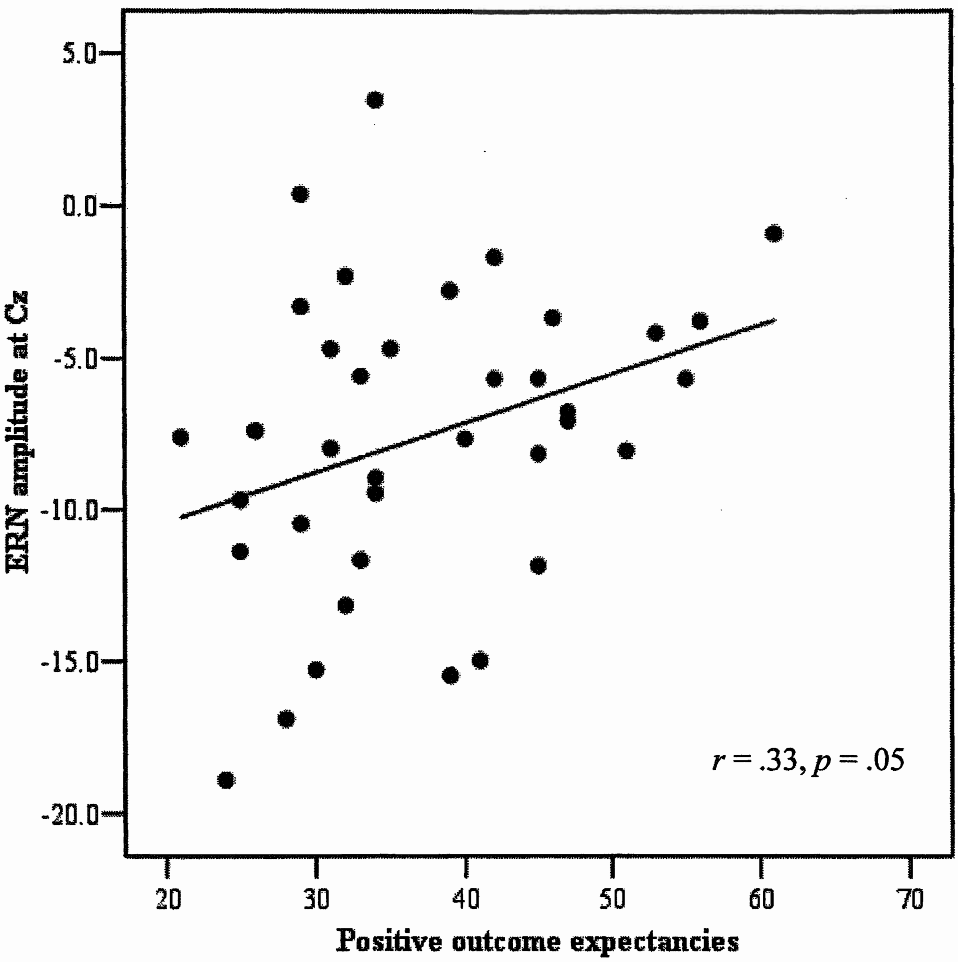

5.0
0.0
-5.0
-10.0
-15.0
-20.0
ERN amplitude at Cz
r = .33, p = .05
20
30
40
50
60
70
Positive outcome expectancies

Figure 3.2

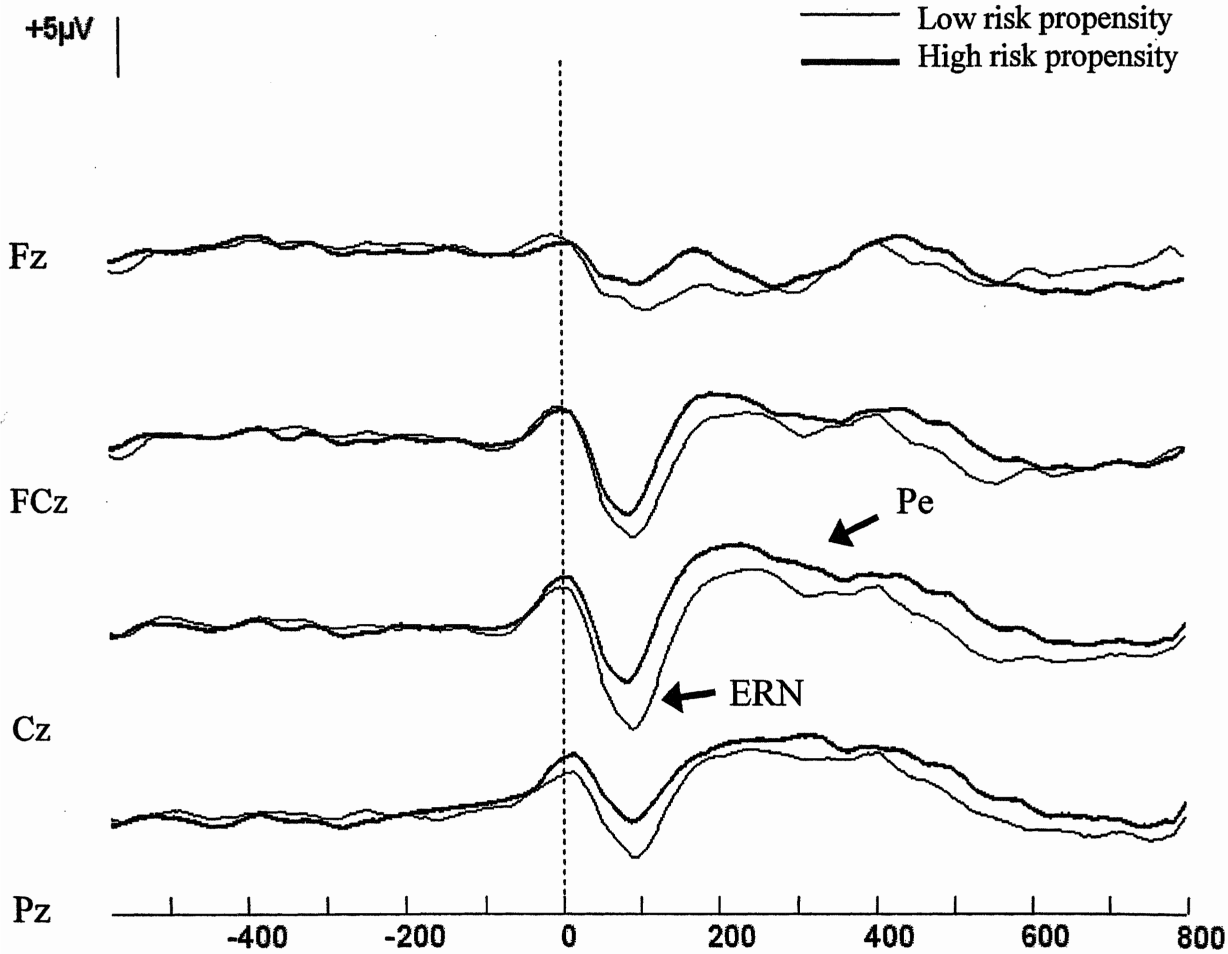

+5µV
Low risk propensity
High risk propensity
Fz
FCz
Pe
Cz
ERN
Pz
-400
-200
0
200
400
600
800

Figure 3.3

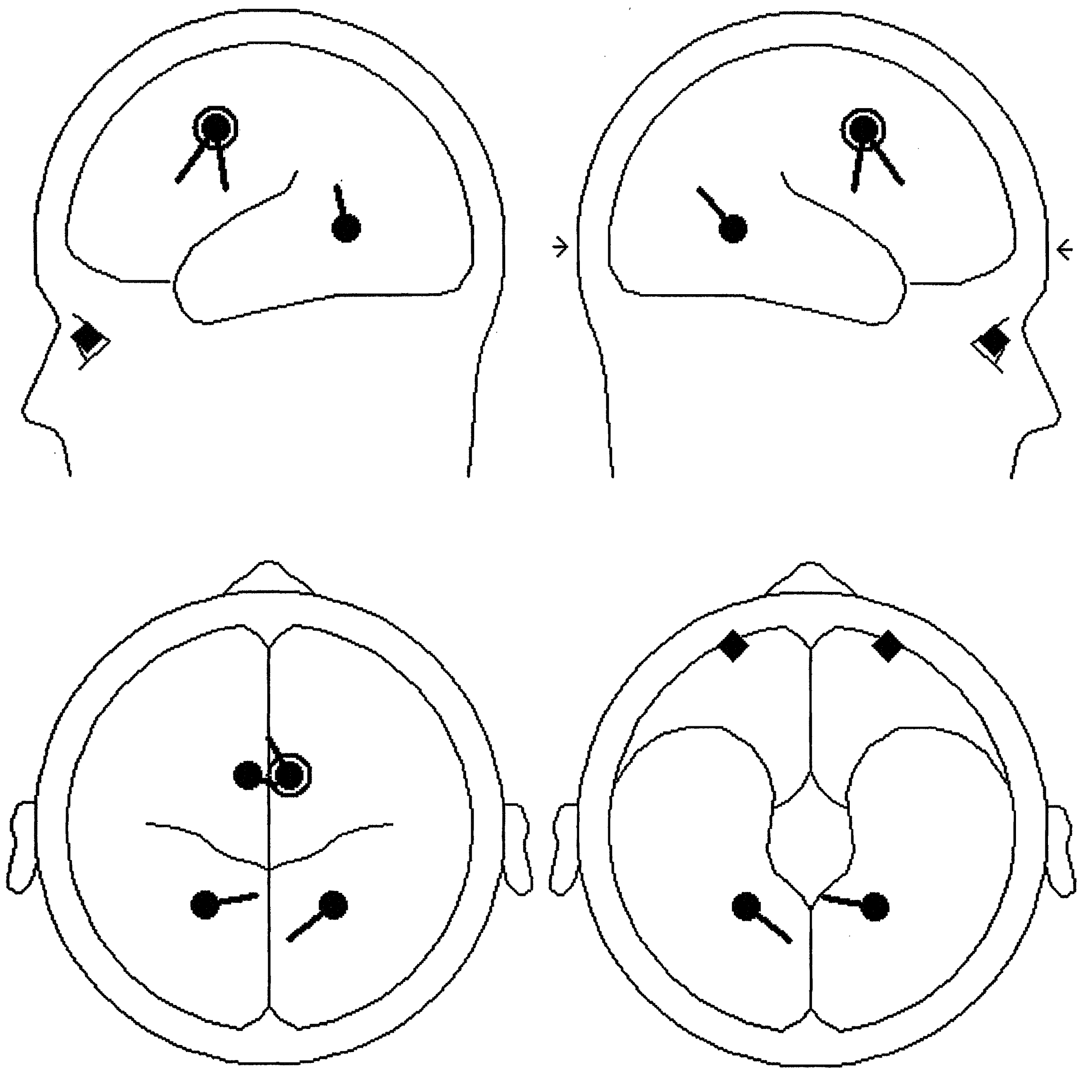


Figure 4.1A

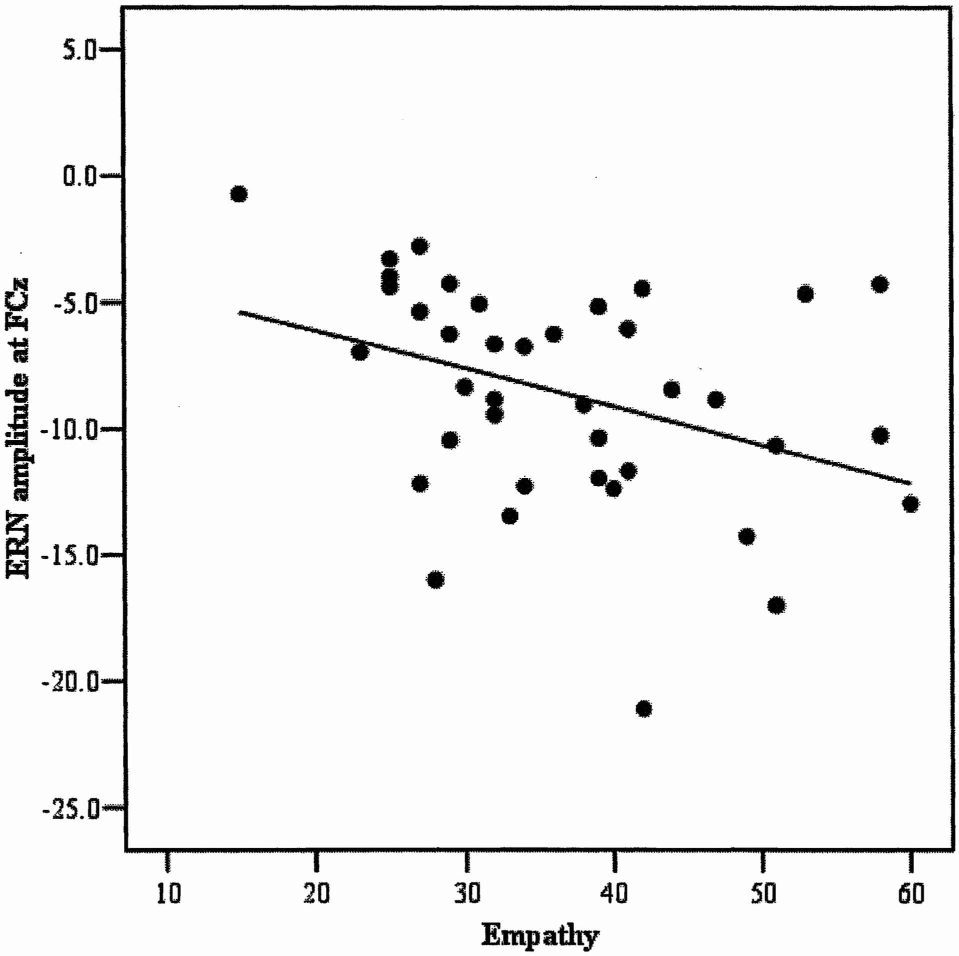

5.0
0.0
-5.0
-10.0
-15.0
-20.0
-25.0
ERN amplitude at FCz
10
20
30
40
50
60
Empathy

Figure 4.1B

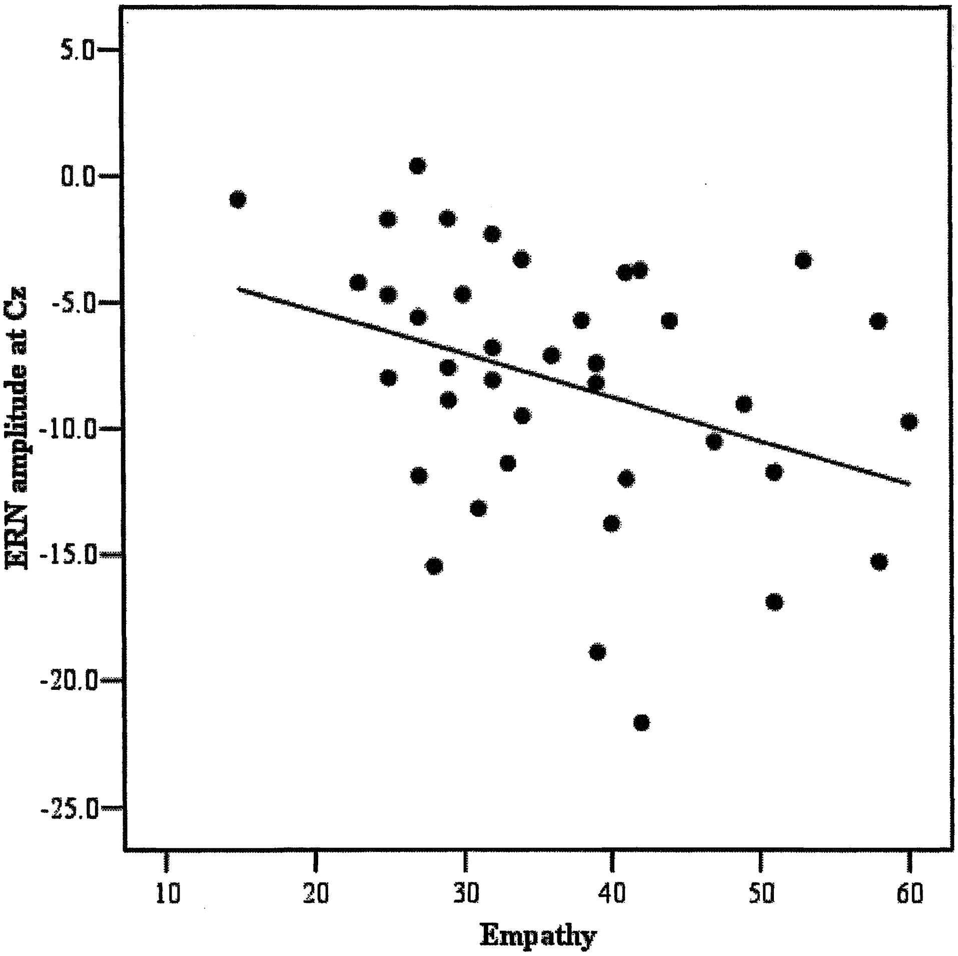

5.0
0.0
-5.0
-10.0
-15.0
-20.0
-25.0
ERN amplitude at Cz
10
20
30
40
50
60
Empathy

Figure 4.2

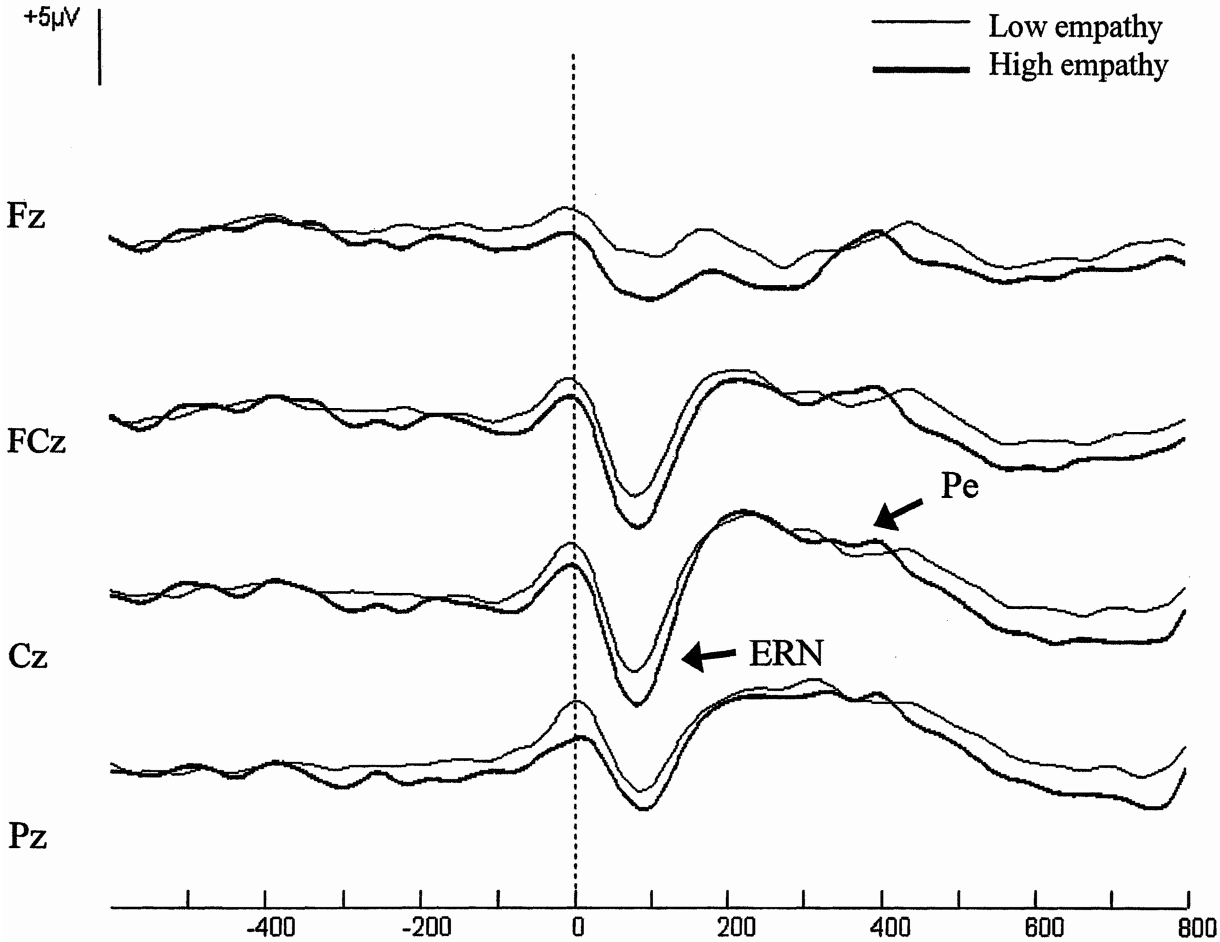

+5µV
Low empathy
High empathy
Fz
FCz
Cz
Pz
Pe
ERN
-400
-200
0
200
400
600
800

Figure 4.3A

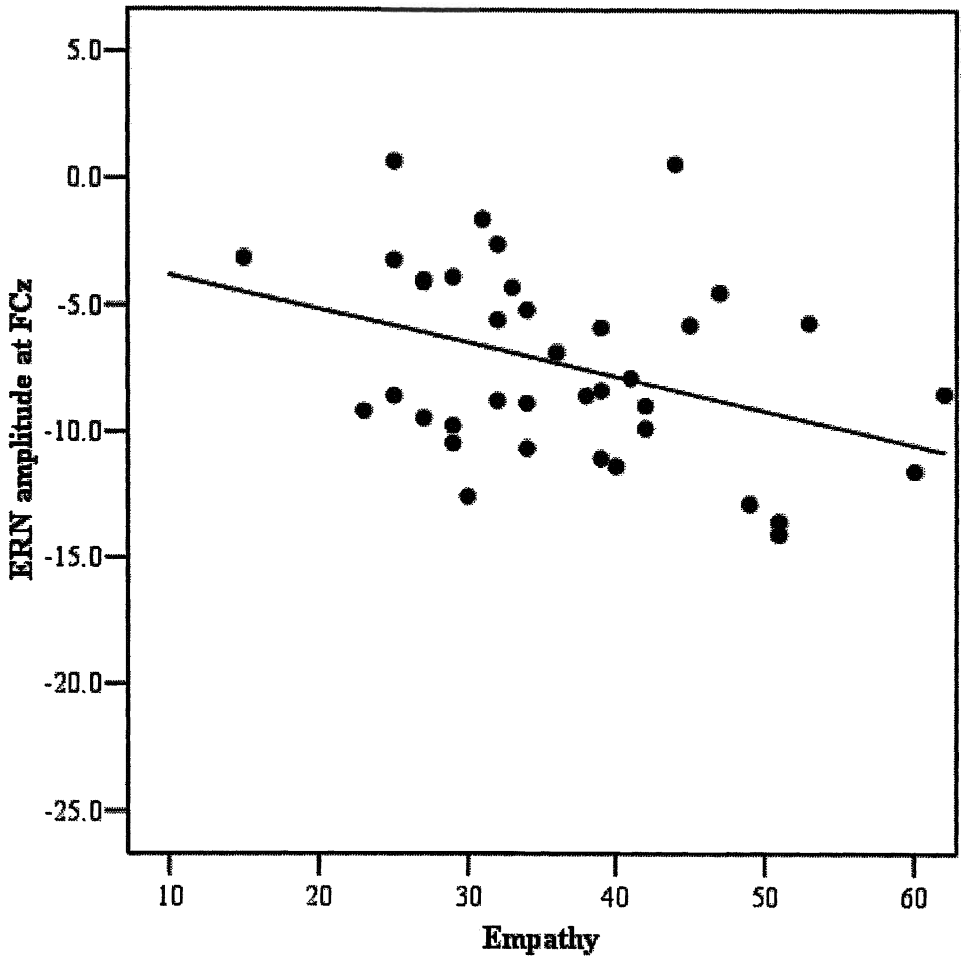

5.0
0.0
-5.0
-10.0
-15.0
-20.0
-25.0
ERN amplitude at FCz
10
20
30
40
50
60
Empathy

Figure 4.3B

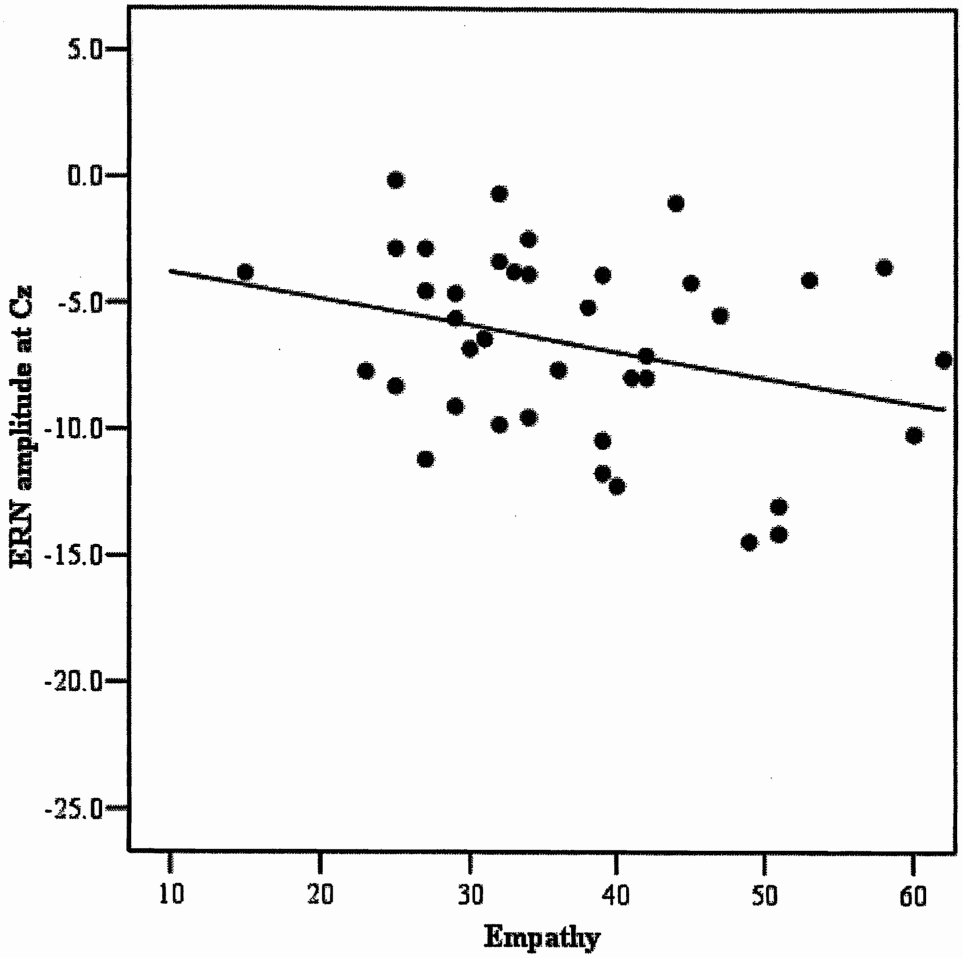
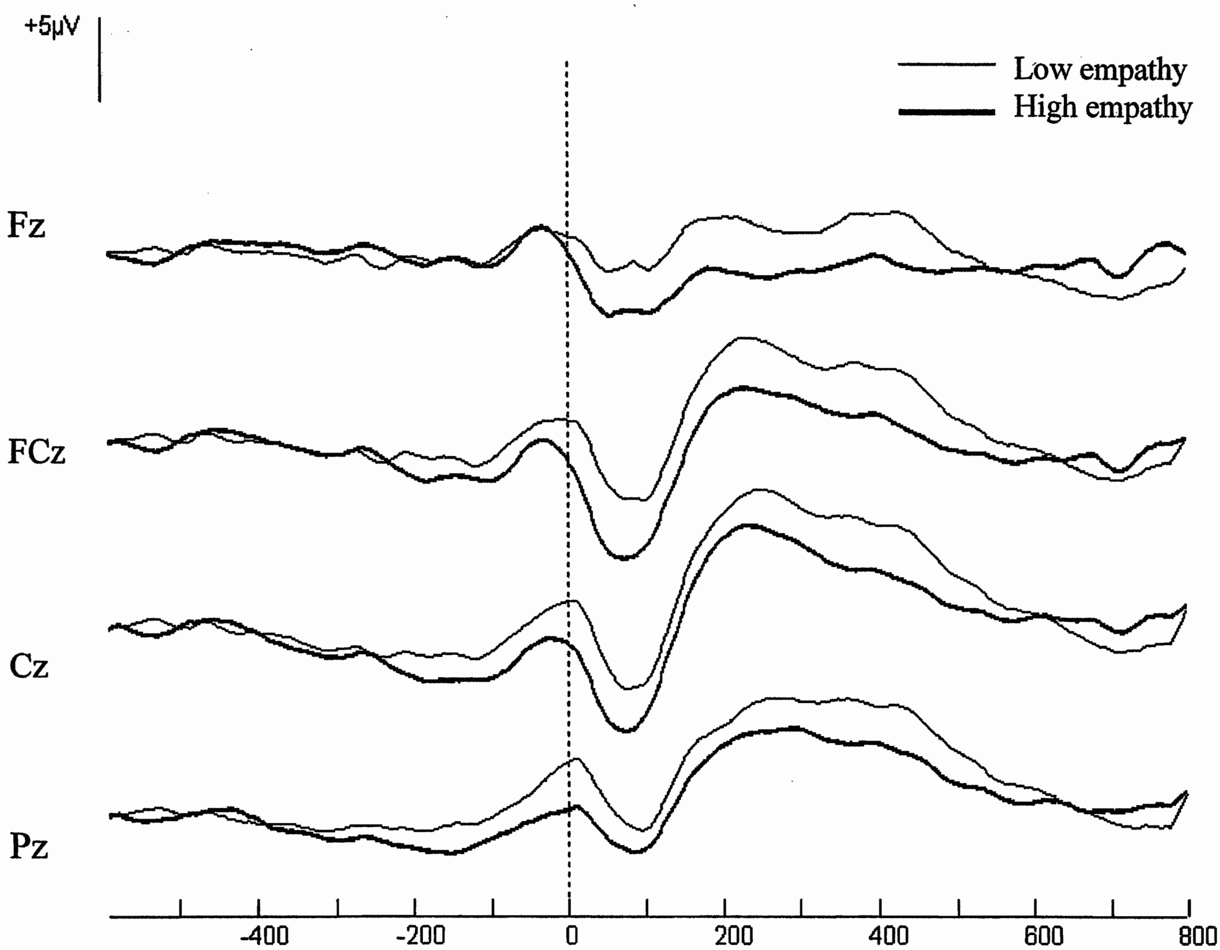

5.0
0.0
-5.0
-10.0
-15.0
-20.0
-25.0
ERN amplitude at Cz
10
20
30
40
50
60
Empathy

Figure 4.4


+5μV
Low empathy
High empathy
Fz
FCz
Cz
Pz
-400
-200
0
200
400
600
800

Appendix A

Directions: Please indicate, how often **within the past 6 months** you engaged in the following activities. Circle your answer.

0	1	2	3	4
Never	**1 time**	**2 – 5 times**	**5 – 9 times**	**10 or more times**

1.	Did not complete an assignment.	0	1	2	3	4
2.	Went rock climbing or mountain climbing.	0	1	2	3	4
3.	Smoked cigarettes or marijuana.	0	1	2	3	4
4.	Grabbed, pushed, or shoved someone.	0	1	2	3	4
5.	Left a social event with someone you just met.	0	1	2	3	4
6.	Did not study for an exam or quiz.	0	1	2	3	4
7.	Punched or hit someone with your fist.	0	1	2	3	4
8.	Mixed drugs and alcohol.	0	1	2	3	4
9.	Damaged or destroyed public property.	0	1	2	3	4
10.	Used drugs other than alcohol or marijuana (e.g., cocaine, ecstasy, speed).	0	1	2	3	4
11.	Had sex without a condom.	0	1	2	3	4
12.	Went skateboarding or in-line skating.	0	1	2	3	4
13.	Did not study or work hard enough.	0	1	2	3	4
14.	Went snow or water skiing.	0	1	2	3	4
15.	Hit someone with a weapon or an object.	0	1	2	3	4
16.	Got into a physical fight.	0	1	2	3	4
17.	Abused prescription drugs.	0	1	2	3	4
18.	Missed/skipped class or work.	0	1	2	3	4
19.	Rode with a drunk driver.	0	1	2	3	4
20.	Drank alcohol.	0	1	2	3	4
21.	Walked alone at night.	0	1	2	3	4
22.	Rode without a seatbelt.	0	1	2	3	4
23.	Got drunk or drank > 5 drinks on one occasion.	0	1	2	3	4
24.	Rode a motorcycle.	0	1	2	3	4
25.	Shoplifted.	0	1	2	3	4

Appendix B

Directions: Each statement can be answered **True** or **False**. Read the statement and decide whether the statement describes you. **Circle** the appropriate answer.

1. I often wish I could be a mountain climber.................................. True False
2. I like some of the earthy body smells.. True False
3. I can't stand watching a movie that I've seen before...................... True False
4. I like wild "uninhibited" parties... True False
5. I like to explore a strange city or section of town myself, even if it means getting lost... True False
6. I get bored seeing the same old faces. ....True False
7. I sometimes like to do things that are a little frightening................. True False
8. People should dress in individual ways even if the effects are sometimes strange...True False
9. I would like to take off on a trip with no pre-planned or definite routes or timetables...True False
10. I get very restless if I have to stay around home for any length of times True False
11. I have no patience with dull or boring persons........................... True False
12. I would like to learn to fly an airplane.......................................True False
13. I would like to meet some persons who are homosexual.................. True False
14. When you can predict almost everything a person will do and say, he or she must be a bore.. True False
15. I often like to get high (drinking liquor or smoking marijuana)........... True False
16. I would like to go scuba diving..True False
17. I have tried marijuana or would like to.......................................True False
18. I usually don't enjoy a movie or play where I can predict what will happen in advance.. True False
19. I could conceive of myself seeking pleasures around the world with the "jet set"... True False
20. I would like to try some of the new drugs that produce hallucination......True False
21. I would like to take up the sport of water skiing.......................... True False
22. I like to try new foods that I have never tasted before..................... True False
23. I enjoy watching many of the "sexy" scenes in movies.................... True False
24. The worst social sin is to be a bore.. True False
25. I often find beauty in the "clashing" of colours and irregular form of modern painting.. True False

26. I think I would enjoy the sensations of skiing very fast down a high mountain slope........ True False
27. I would like to try parachuting jumping........ True False
28. Looking at someone's home movies/ travel slides bores me........ True False
29. Keeping the drinks full is the key to a good party........ True False
30. I would like to sail a long distance in a small but seaworthy sailing craft. True False
31. I would like to make friends in some of the "far-out" groups like artists or "hippies"........ True False
32. I feel best after taking a couple of drinks........ True False
33. I would like to try surfboard riding........True False
34. I enjoy the company of real "swingers"........True False
35. I like people who are sharp and witty even if they do sometimes insult others........ True False
36. I like to have new and exciting experiences and sensations even it they are a little unconventional or illegal........True False
37. I like to dive off the high board........ True False
38. A person should have considerable sexual experience before marriage.. True False
39. I prefer friends who are excitingly unpredictable........ True False
40. I like to date people who are physically exciting........ True False

Appendix C

Directions: Please read each statement and circle **Yes** or **No** if the statement describes you.

1. Do you often refrain from doing something because you are afraid of it being illegal?.... YES NO
2. Does the good prospect of obtaining money motivate you strongly to do some things?..... YES NO
3. Do you prefer not to ask for something when you are not sure you will get it?............. YES NO
4. Are you frequently encouraged to act by the possibility of being valued in your work?..... YES NO
5. Are you often afraid of new or unexpected situations?.. YES NO
6. Do you often meet people that you find physically attractive?................................ YES NO
7. Is it difficult for you to telephone someone you do not know?................................ YES NO
8. Do you like to take some drugs because of the pleasure you get from them?.............. YES NO
9. Do you often give up your rights when you know you can avoid a quarrel with a person?.. YES NO
10. Do you often do things to be praised?.. YES NO
11. As a child, were you troubled by punishments at home or in school?......................... YES NO
12. Do you like being the centre of attention at a party or social meeting?..................... YES NO
13. In tasks that you are not prepared for, do you attach great importance to the possibility of failure?.. YES NO
14. Do you spend a lot of your time on obtaining a good image?................................ YES NO
15. Are you easily discouraged in difficult situations?... YES NO
16. Do you need people to show their affection for you all the time?............................ YES NO
17. Are you a shy person? .... YES NO
18. When you are in a group, do you try to make your opinions the most intelligent or funniest?.. YES NO
19. Whenever possible, do you avoid demonstrating your skills for fear of being embarrassed?.. YES NO
20. Do you often take the opportunity to pick up people you find attractive?.................. YES NO
21. When you are with a group, do you have difficulties selecting a good topic to talk about?. YES NO
22. As a child, did you do a lot of things to get peoples' approval?............................... YES NO
23. Is it often difficult for you to fall asleep when you thing about things you have done or must do?.. YES NO
24. Does the possibility of social advancement ("moving up the social ladder") make you do things, even if this involves not playing fair? .... YES NO
25. Do you think a lot before complaining in a restaurant if your meal is not well prepared?... YES NO
26. Do you prefer activities that have an immediate gain?.. YES NO

27. Would you be bothered if you had to return to a store if you were given the wrong change?...YES NO
28. Do you often have trouble resisting the temptation of doing forbidden things?... YES NO
29. Whenever you can, do you avoid going to unknown places? ... YES NO
30. Do you like to compete and do everything you can to win?...YES NO
31. Are you often worried by things that you said or did?... YES NO
32. Is it easy for you to associate tastes and smells to very pleasant events?... YES NO
33. Would it be difficulty for you to ask your boss for a raise (salary increase)?...YES NO
34. Are there a large number of objects or sensations that remind you of pleasant things?..... YES NO
35. Do you generally try to avoid speaking in public?... YES NO
36. When you start to play with a slot machine, is it often difficult for you to stop?...YES NO
37. Do you, on a regular basis, think that you could do more things if it was not for your insecurity or fear?... YES NO
38. Do you sometimes do things for quick gains?... YES NO
39. Comparing yourself to people you know, are you afraid of many things?... YES NO
40. Does your attention easily stray from your work in the presence of an attractive stranger? YES NO
41. Do you often find yourself worrying about things so much that it disrupts your thinking? YES NO
42. Are you interested in money to the point of being able to do risky jobs?... YES NO
43. Do you avoid doing some things you like in order not to be rejected or disapproved by others?... YES NO
44. Do you make most activities competitive?...YES NO
45. Generally, do you pay more attention to threats than to pleasant events?... YES NO
46. Would you like to be a socially powerful person?... YES NO
47. Do you often refrain from doing something because of your fear of being embarrassed?...YES NO
48. Do you like displaying your physical abilities even though this may involve danger? ......YES NO

Appendix D

Directions: Read each statement carefully and rate how strongly you agree and disagree with it. Use the following scale.

1	2	3	4
Strongly Agree	**Slightly Agree**	**Slightly Disagree**	**Strongly Disagree**

1. I can easily tell if someone else wants to enter a conversation.	1	2	3	4
2. I prefer animals to humans.	1	2	3	4
3. I try to keep up with the current trends and fashions.	1	2	3	4
4. I find it difficult to explain to others, things that I don't understand easily, when they don't understand it the first time.	1	2	3	4
5. I dream most nights.	1	2	3	4
6. I really enjoy caring for other people.	1	2	3	4
7. I try to solve my own problems rather than discussing them with others.	1	2	3	4
8. I find it hard to know what to do in a social situation.	1	2	3	4
9. I am at my best first thing in the morning.	1	2	3	4
10. People often tell me that I went too far when driving my point home in a discussion.	1	2	3	4
11. It doesn't bother me too much if I am late meeting a friend.	1	2	3	4
12. Friendships and relationships are just too difficult, so I tend not to bother with them.	1	2	3	4
13. I would never break a law, no matter how minor.	1	2	3	4
14. I often find it difficult to judge if something is rude or polite.	1	2	3	4
15. In a conversation, I tend to focus on my own thoughts rather than on what my listener might be thinking.	1	2	3	4
16. I prefer practical jokes to verbal humor.	1	2	3	4
17. I live life for today rather than for the future.	1	2	3	4
18. When I was a child, I enjoyed cutting up worms to see what would happen.	1	2	3	4

19. I can pick up quickly if someone says one thing but means another.	1	2	3	4
20. I tend to have very strong opinions about morality.	1	2	3	4
21. It is hard for me to see why some things upset people so much.	1	2	3	4
22. I find it easy to put myself in someone else's shoes.	1	2	3	4
23. I think that good manners are the most important thing a parent can teach their child.	1	2	3	4
24. I like to do things on the spur of the moment.	1	2	3	4
25. I am good at predicting how someone will feel.	1	2	3	4
26. I am quick to spot when someone in a group is feeling awkward or uncomfortable.	1	2	3	4
27. If I say something that someone else is offended by, I think that's their problem, not mine.	1	2	3	4
28. If anyone asked me if I liked their haircut, I would reply truthfully, even if I didn't like it.	1	2	3	4
29. I can't always see why someone should have felt offended by a remark.	1	2	3	4
30. People often tell me that I am very unpredictable.	1	2	3	4
31. I enjoy being the center of attention at any social gathering.	1	2	3	4
32. Seeing people cry doesn't really upset me.	1	2	3	4
33. I enjoy having discussions about politics.	1	2	3	4
34. I am very blunt, which some people take to be rudeness, even though this is unintentional.	1	2	3	4
35. I don't tend to find social situations confusing.	1	2	3	4
36. Other people tell me that I am good at understanding how they are feeling and what they are thinking.	1	2	3	4
37. When I talk to people, I tend to talk about their experiences rather than my own.	1	2	3	4
38. It upsets me to see an animal in pain.	1	2	3	4
39. I'm able to make decisions without being influenced by people's feelings.	1	2	3	4
40. I can't relax until I have done everything I had planned to do that day.	1	2	3	4

41. I can easily tell if someone else is interested or bored with what I am saying.	1	2	3	4
42. I get upset if I see people suffering on news programs.	1	2	3	4
43. Friends usually talk to me about their problems as they say that I am very understanding.	1	2	3	4
44. I can sense if I am intruding, even if the other person doesn't tell me.	1	2	3	4
45. I often start new hobbies but quickly become bored with them and move on to something else.	1	2	3	4
46. People sometimes tell me that I have gone too far with teasing.	1	2	3	4
47. I would be too nervous to go on a big roller coaster.	1	2	3	4
48. Other people often say that I am insensitive, though I don't always see why.	1	2	3	4
49. If I see a stranger in a group, I think that it is up to them to make an effort to join in.	1	2	3	4
50. I usually stay emotionally detached when watching a film.	1	2	3	4
51. I like to be very organized in day-to-day life and often make lists of the chores I have to do.	1	2	3	4
52. I can tune in to how someone else feels rapidly and intuitively.	1	2	3	4
53. I don't like to take risks.	1	2	3	4
54. I can easily work out what another person might want to talk about.	1	2	3	4
55. I can tell if someone is masking their true emotion.	1	2	3	4
56. Before making a decision I always weigh the pros and cons.	1	2	3	4
57. I don't consciously work out the rules of social situations.	1	2	3	4
58. I am good at predicting what someone will do.	1	2	3	4
59. I tend to get emotionally involved with a friend's problems.	1	2	3	4
60. I can usually appreciate the other person's viewpoint, even if I don't agree with it.	1	2	3	4